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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III.
A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS

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Artocarpus J. R. & G. Forster, Char. Gen. 101. *t.* 51, 51a. 1776, nomen conservandum; Linn. f. Suppl. Pl. 61, 411. 1781; Lamarck, Encycl. Méth. 3: 207. 1789; Willd. Sp. Pl. ed. 4. 4: 188. 1805; Persoon, Syn. Pl. 2: 531. 1807; Blume, Bijdr. 479. 1825; Roxb. Fl. Ind. 3: 521. 1832; Blanco, Fl. Filip. 666. 1837, "*Arctocarpus*"; Trécul, Ann. Sci. Nat. Bot. III. 8: 109. 1847; Miq. Fl. Ind. Bat. 1(2): 284. 1859, Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867; King in Hook. f. Fl. Brit. Ind. 5: 539. 1888; King, Ann. Bot. Gard. Calcutta 2: 1. 1889; Becc. For. Borneo, 625. 1902; Renner, Bot. Jahrb. 39: 363. 1907; Elmer, Leaflet. Philip. Bot. 2: 609. 1909; Gagnep. Bull. Soc. Bot. Fr. 73: 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 731. 1928; Corner, Wayside Trees of Malaya, 649. 1940; Jarrett, Jour. Arnold Arb. 40: 8, 11. *fig. 1, f-k, fig. 3, d-f.* 1959. TYPE SPECIES: *Artocarpus communis* J. R. & G. Forster.

Saccus or *Soccus* Rumph. Herb. Amb. 1: 104-115. *t.* 30-34. 1741.

Sitodium [Banks & Solander ex] Parkinson, Jour. Voy. Endeavour, 45. 1773, nomen subnudum.

Rademachia Thunb. Vet. Akad. Handl. Stockholm 37: 251. 1776; Houttuyn, Nat. Hist. II. Pl. 11: 446. 1779. TYPE SPECIES: *Rademachia incisa* Thunb. (= *Artocarpus communis* J. R. & G. Forster).

Sitodium [Banks & Solander ex] Thunb. Philos. Trans. Roy. Soc. London 69: 465. 1779, nomen illegitimum.

Sitodium Banks [& Solander] ex Gaertn. Fruct. 1: 344. *t.* 71, 72. 1788, nomen illegitimum.

Polyphema Lour. Fl. Cochinch. 546. 1790. TYPE SPECIES: *Polyphema jaca* Lour. (= *Artocarpus heterophyllus* Lamarck).

Saccus O. Kuntze, Rev. Gen. 633. 1891, nomen illegitimum.

Small to large trees. *Leaves* spirally arranged (subg. *Artocarpus*) or alternate and distichous (subg. *Pseudojaca*), simple and entire to pinnatifid, or pinnate (*A. anisophyllus*), penninerved (basally trinerved in *A. altissimus*), thinly to thickly coriaceous, glabrous to pubescent or hispid; epidermal gland-hairs superficial to deeply immersed, heads globose to

flattened and peltate, 1–16-celled; spongy mesophyll long-armed and usually very loose (subg. *Artocarpus*), with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*), or compact, lacking resin-cells (subg. *Pseudojaca*); juvenile leaves entire to pinnatifid, or pinnate (*A. tamaran*), or with the lamina reduced to a sinuous wing along the midrib. *Stipules* paired, large, intrapetiolar, amplexicaul, scars annulate (subg. *Artocarpus*) or small, non-amplexicaul, scars lateral or intrapetiolar (subg. *Pseudojaca*).

Inflorescences unisexual, capitate, head cylindrical to clavate, obovoid, ellipsoid or globose, lobed (in syncarp) or not, pedunculate (rarely subsessile), solitary or paired in leaf-axils, rarely borne on short shoots on older wood (subg. *Pseudojaca*) or rami- or cauliflorous (*A. integer*, *A. heterophyllus*); numerous flowers compactly covering surface, the perianths enclosing a single ovary or stamen, mixed with abundant stalked, peltate, varying to clavate or spatulate interfloral bracts, these often caducous from syncarp, or in some species entirely lacking, or in one (*A. styracifolius*) enlarging to form flexuous processes on syncarp; involucre absent (top of peduncle forming an annulus in *A. heterophyllus*). *At anthesis: male head* with perianths tubular and bilobed or perforate above, to 2–4-partite, stamens short- to long-exserted, anther-cells globose to oblong; *female head* with perianths tubular, thin-walled below and enclosing ovary, thick-walled above with a narrow lumen containing the style, partially or completely (in some species of subg. *Pseudojaca*) fused with one another to form syncarp; partial fusion occurring only between distal thick-walled region of perianths to form an external wall, with proximal thin-walled region remaining free; perianths completely fused above to form a smooth or areolate surface with the styles exerted through perforations, or the apices free, forming cylindrical, conical, umbonate or truncate, rigid or flexuous processes on surface, all with styles exerted from their tips, or some processes sterile (in some species of subg. *Artocarpus*), solid, elongate and projecting beyond the rest (some of these species also with sterile, solid, elongate flowers in the male head); ovary unilocular, the style apical to lateral, simple or bifid (branches sometimes very unequal), the ovule subapical to lateral. *Mature syncarp* formed by the enlargement of the entire female head, with one to many flowers forming fruit; proximal portions of fruiting perianths, if free, either becoming fleshy or not, the remaining perianths elongated and ribbon-like; mature ovary thin-walled to fleshy or horny, or developing an indurated endocarp freed by decay of rest of wall, the style apical to sub-basal, the seed large, attached subapically to sub-basally, testa membranous to pergamaceous, endosperm none, the embryo straight, orientation longitudinal or oblique, cotyledons equal or not, appressed faces at an angle of 0–90° to median plane of ovary, radicle and plumule small to minute, apical or lateral; germination hypogeal.

DISTRIBUTION: Ceylon, India, Pakistan, Burma, Siam, Indochina, southern China, Malaysia, Solomon Islands; two species (*A. communis*, *A. heterophyllus*) cultivated throughout the tropics.

HISTORY OF THE GENUS AND NOMENCLATURE OF BREADFRUIT,
CHEMPEDAK AND JACK

The genus *Artocarpus* is represented by indigenous species in an area extending from India and Ceylon to southern China, and through Malaysia to the Solomon Islands, while two species — the Breadfruit and the Jack — are now cultivated throughout the tropics. That it was, nevertheless, unknown to Linnaeus is somewhat surprising in view of the distinctiveness and economic importance of some of the species and the excellent descriptions which they had received from earlier authors.

The Jack was probably briefly mentioned by Theophrastus in about 300 B.C. as occurring in India and it figured more extensively in many later travellers' tales. The Breadfruit was first mentioned at the end of the sixteenth century by voyagers in the Pacific, where it was already widespread and of great importance to the Polynesians; it was recorded as far west as Java in 1642 and had become circumtropical in cultivation at least by the close of the eighteenth century.

PRE-LINNAEAN BOTANICAL DESCRIPTIONS. Among early botanical writers, Rheede described in 1682 both the Jack, which was already cultivated through most of tropical Asia and Malaysia, and a species of the Western Ghats, *Artocarpus hirsutus*, under the vernacular names *Tsjaka-maram* and *Ansjeli* (Hort. Ind. Malab. 3: 17, 25. t. 26–28, 32). At about the same time Rumphius prepared very full descriptions of the Jack and the Chempedak (then, as now, almost restricted to and less commonly cultivated in Malaysia) as *Saccus arboreus major* and *S. a. minor*; of the seedless and seeded forms of the Breadfruit and an allied wild species of the Moluccas as *Soccus* [sic] *lanosus*, *S. granosus* and *S. silvestris*, respectively; and, finally, of another Malaysian species, *Artocarpus fretissii*, as *Metrosideros spuria* (Herb. Amb. 1: 104–115. t. 30–34. 1741, 3: 26. t. 13. 1743). These are the most important pre-Linnaean botanical references to members of the genus, but several species from the Philippines were listed under their vernacular names, with brief descriptions, by J. G. Kamel (in Ray, Hist. Pl. 3, App. 51, 52. 1704). No attempt was made to identify Rumphius' plants by Linnaeus in 1754 (Herb. Amb. [resp. O. Stickman]), except for *Metrosideros spuria*, which he wrongly equated with *Ochna jabotapita* L. Nor did Burman provide any further identifications in his indices to the "Herbarium Amboinense" published in 1755 and 1769.

In 1891 Kuntze held that the generic name *Saccus* had been validly published by Rumphius and, accordingly, he made many new combinations under it. These are illegitimate, however, and are omitted from the synonymy of the various species.

POST-LINNAEAN BOTANICAL DESCRIPTIONS. Once the genus had become known to post-Linnaean botanists, it was described, within about twenty years, under four different generic names, *Sitodium* (1773, 1779 and 1788), *Artocarpus* (1776), *Rademachia* (1776) and *Polyphema* (1790), but the

name *Artocarpus* has been in continuous and undisputed use until doubt recently arose as to its priority, resulting in its conservation over *Sitodium* (1773). A review of the facts concerning these various publications follows, in which an attempt is made to determine their status and hence to establish whether the conservation of *Artocarpus* was necessary. This review is extended to cover the nomenclature of the Breadfruit, Chempedak and Jack — the only species in which any serious problems have arisen — since this will involve the addition of only two items to the material literature and will avoid later repetition, as well as provide a detailed picture of the early botanical history of the genus. Except for the earliest description of *Sitodium* and Houttuyn's publication of *Rademachia* the discussion will be largely based on the two papers published by Corner in 1939, although all the references have been carefully re-examined. For each name the Rumphian and post-Linnaean synonyms cited will be given and the factors taken into consideration in deciding its status will be clearly stated.

SITODIUM, ARTOCARPUS AND RADEMACHIA. The Breadfruit was the first species of the genus of which a description was published under a Linnaean binomial. This was done, under the name *Sitodium-altile* [sic], by Stanfield Parkinson in 1773 in his edition of "A Journal of a Voyage to the South Seas, in His Majesty's Ship, The Endeavour," which was written by his brother Sydney, who accompanied Sir Joseph Banks and Dr. Solander as an artist on Cook's first voyage around the world (1768–1771) but died on the way home from Batavia. In this was included a series of notes on plants seen in Tahiti, to most of which were appended, without acknowledgement, hyphenated "Latin names" corresponding to the binomials in Solander's manuscript "Primitiae Florae Insularum Oceani Pacifici, . . ." now in the British Museum (Natural History), London. This journal had been generally overlooked until Fosberg drew attention to it in 1939 (*Am. Jour. Bot.* 26: 229–231) and stated that Parkinson's description would necessitate the conservation of *Artocarpus* over *Sitodium*, which was finally achieved on these grounds in 1955 (*Taxon* 4: 162. 1955). In anticipation of this action the new combination *Artocarpus altilis* (Parkinson) Fosberg was published by him in 1941 (*Jour. Wash. Acad. Sci.* 31: 95) as the correct name for the Breadfruit.

However, Sydney Parkinson's notes are totally unscientific and mostly very brief; he was apparently quite unaware of the significance of his action in using those of the binomials that were new, as was his brother in publishing them, and few of them have any claim at all to valid publication. The account of the Breadfruit happens to be rather longer than the others but is merely a general description of which the "botanical" part is given below.

E ooroo

Sitodium-altile.

. . . This tree grows to between thirty and forty feet high, has large palmated leaves, of a deep grass-green on the upper-side, but paler on the under; and bears male and female flowers, which come out single at the bottom or joint of each leaf. The male flower fades and drops off; the female, or cluster of females,

swell and yield the fruit, which often weighs three or four pounds, and is as big as a person's head when full grown. It is of a green colour; the rind is divided into a number of polygonal sections; the general shape a little longer than round, and white on the inside, with a pretty large core. The fruit, as well as the whole plant, is full of a white clammy juice, which issues plentifully from any part that is cut: . . .

In order for this description to be validly published it would have to be adequate as a "generico-specific" description, as was pointed out by Dandy and Exell *in litt.*, cited by Merrill (The Botany of Cook's Voyages. Chron. Bot. 14: 330. 1954) in the course of a detailed discussion of Parkinson's journal. Merrill's view that the description is not valid seems fully justified, the more so if the circumstances of publication are taken into consideration. This question must, however, always remain a matter of opinion and, since it has now been settled, for any who feel that they must recognize the validity of Parkinson's description, by conservation, its chief importance is in determining the specific epithet to be applied to the Breadfruit. The source of the generic name *Sitodium* is nowhere directly indicated in the literature of the eighteenth century, but it is now generally recognized that the authors should be cited as [Banks & Solander ex] (or [Solander ex]) Parkinson, etc.

A botanical description of the Breadfruit was published in 1776 under the name *Artocarpus communis*, with *Soccus* [*lanosus* and *granosus*] in synonymy, by J. R. & G. Forster, who were the botanists on Cook's second voyage around the world (1772-1775) (the generic name being derived from the Greek *artos*, bread, and *karpos*, fruit). In the same year another description of the Breadfruit, together with one of the Chempedak, was published under the generic name *Rademachia*, with the specific epithets *incisa* (synonyms: *Soccus lanosus*, *S. granosus* and *S. silvestris*) and *integra* (synonyms: *Soccus arboreus major* and *S. a. minor*), respectively, by C. P. Thunberg in a paper dated Batavia, d.15 Junii 1775. The name was given in honour of Herr Radermacher, then "Baillou" of Batavia, from whom Thunberg received much assistance, especially later, when he returned from Japan. It has not been possible to determine which of these two names was published first. The preface to the Forsters' "Characteres Generum Plantarum" was dated November 1775, and there is no reason to doubt that the title-page is correct in giving the date as 1776, but no more precise evidence is available. Thunberg's description was published in the July-September issue of the Kongl. Vetenskaps Acadamiens Handlingar for 1776, but Merrill (l.c., 359) stated that Hultén had been unable to find any record of the date of publication in Stockholm. Although it seems likely that *Artocarpus* was actually published before *Rademachia*, unless this can be established, the first person to choose between the two names must be followed. It has always been assumed that this choice was made by Linnaeus *filius* in 1781 in his "Supplementum Plantarum" when he used the name *Artocarpus*, combining both generic descriptions, though without giving *Rademachia* as a synonym. He recognized two species, *A. incisus* and *A. integrifolia* [sic], basing his descriptions on those of Thun-

berg and citing his names, and the same Rumphian names, but not *A. communis*, in synonymy.

It has, however, been overlooked that in 1779 Houttuyn had republished, in an account entitled "Beschryving van den Oostindischen Broodboom" which he included in his "Natuurlyke Historie," Thunberg's description of *Rademachia* (from a manuscript in Thunberg's hand sent to him by Radermacher) and had chosen his name to replace that of the Forsters on the grounds that the description was more complete, in that the formation of seeds was mentioned, whereas the description of *Artocarpus* was based solely on the seedless form of the Breadfruit. Houttuyn cited "*Artocarpus*" in synonymy under *Rademachia incisa*, in addition to the Rumphian names, and this would certainly have necessitated the conservation of *Artocarpus* over *Rademachia*, but for the fact that he did not know of the earlier publication of Thunberg's name in Sweden and hence was, giving his state of knowledge and intentions priority over the fortuitous circumstances, acting in contravention of present-day rules of nomenclature. Houttuyn's specific descriptions were based, in part at least, on material sent to him by Radermacher and, from his account of *Rademachia integra*, it seems that he had received the foliage of the Chempedak, but the fruit of the Jack. He also described very briefly a third species, *R. rotunda* (*Artocarpus rotunda* (Houtt.) Panzer, Pflanzensyst. 10: 380. 1783; in a translated and amplified version of Houttuyn's paper), which it has not been possible to identify, although Merrill (Jour. Arnold Arb. 19: 331. 1938) reduced *Artocarpus rigidus* to synonymy under Panzer's name. *Rademachia rotunda* will therefore be discussed further under that species. (Merrill did not comment on Houttuyn's reduction of *Artocarpus*.)

THE BREADFRUIT. In determining the correct name for the Breadfruit, if the specific epithet *altilis* is rejected as invalidly published and Houttuyn's action is ruled illegitimate, it remains to consider whether the choice made by Linnaeus *filius* in forming the name *Artocarpus incisus* for this plant is legitimate. The use of the name *Artocarpus communis* in its place was first formally recommended by Richter in 1894 (Bot. Centralbl. 60: 169) on the grounds of its priority, and he was followed by various authors, including Merrill. The question was next fully discussed by Corner in 1939 (Gard. Bull. Singapore 10: 280) who concluded that, as the Rules then stood, Linnaeus *filius* was perfectly free, in making the choice between two simultaneously published names, to take the generic name from one genus and the specific epithet from the other (although he had chosen *incisus* over *communis* only by implication, this is all that is now required). According to Article 57 of the International Code of Botanical Nomenclature, 1956, this is still true; there is nothing to indicate that the choice of generic name determines the specific epithet, where both are simultaneously published. Therefore, if the generic names and specific epithets are considered *independently*, the argument is valid and it is only after much deliberation that the decision has been made to reject it in the interests of stability of nomenclature and in order to follow the general principles of the Rules.

In the present example, Article 57 is in conflict with Principles III and IV, especially the latter: "Each taxonomic group can bear only one correct name [which for a species is a binary combination; see Art. 23], the earliest that is in accordance with the Rules," *Artocarpus* became the correct generic name through the choice made by Linnaeus *filius*; thus the earliest *combination* based on the Breadfruit that is in accordance with the Rules is *Artocarpus communis* (1776). The name *Artocarpus incisus* (1781) is also legitimate at present (apparently it is not in conflict with Article 11), but, if any change were considered necessary in Article 57 in order to deal with this unusual problem, the Article would undoubtedly be brought into line with the Principles.

St. John (Pacific Sci. 2: 109. 1948), in the only other detailed consideration of the nomenclature of the Breadfruit, concluded that the name *Artocarpus incisus* should be used, following both Article 57 (then no. 56) and established custom. However, there has been uncertainty as to the correct name of the Breadfruit for over fifty years. *Artocarpus communis* has been gaining gradually in acceptance over *A. incisus* and is now perhaps more widely used. With the addition of *Artocarpus altilis* as a third possibility, the situation has become more confused during the last two decades. It is evident that "established custom" cannot provide a stable solution to the problem. Moreover, in view of the long-standing uncertainty, any argument based on custom has lost much of its force in this particular instance, although the general desirability of following custom, where there is genuine doubt as to the consequences of the Rules, is not questioned. It is regretted that the name *Artocarpus incisus* was used in the first paper of this series.

THE CHEMPEDAK. Turning now to the second species described by Thunberg and Linnaeus *filius*, this was until recently erroneously identified as the Jack, to which the name *Artocarpus integrifolia* was universally applied from the beginning of the nineteenth century until it was partially replaced in the literature by the legitimate combination *A. integer*. This was made by Merrill in 1917 (as *A. integra*, Interpr. Rumph. Herb. Amb. 190), to replace Linnaeus *filius*' superfluous name, and was used by him in his consideration of Rumphian names in the same sense, i.e., as the correct name for *Saccus arboreus major*.

In 1939, however, Corner demonstrated conclusively, in a paper on the distinguishing characters and nomenclature of the Jack and the Chempedak (Gard. Bull. Singapore 10: 56-81. t. 1, 2), that Thunberg's description had been based solely on the Chempedak. Although the latter had cited both *Saccus arboreus major* and *S. a. minor* as synonyms, and had given the Malay name of the tree as *Tjampeda*, but that of the fruit as *Nanca* (the Malay name for the Jack) and thus had, apparently, attributed the fruit of the Jack to the foliage of the Chempedak (as is also indicated by the material received by Houttuyn), only the vegetative parts were included in his description (with a note in Swedish that the roots, stems, branches and flowers were as in the preceding species [*Rademachia incisa*]). From the shape and colour of the leaf and the indumentum of rigid, patent

hairs on the lower surface, twigs and peduncles, Corner showed that the description could refer only to the Chempedak (the Jack being glabrous), so that, in spite of the confusion in the Malayan and Rumphian names, the application of Thunberg's name is unambiguous. The distribution was given by Thunberg as Java, around Batavia, and (from Rumphius) Amboina and other places. Corner stated that Professor Svedelius had examined the type specimen at Uppsala and had found that it consisted of material of the Chempedak agreeing with Thunberg's description and including male inflorescences without the annulus at the base of the head that is found only in the Jack. Mixed with it was material of the Jack (see photographs in Corner, l.c.) which, from the note on the back of the sheet, "e Ceylona Thunberg," had probably been collected in Ceylon, where the Chempedak does not occur (presumably on Thunberg's visit there in 1777-78 on the way back from Batavia). Professor Svedelius thought that by an error the two plants of different origin had been put on the same sheet when Thunberg's collections were mounted some years later. This was confirmed by the discovery, in the course of the present revision, of a sheet in the Rijksherbarium, Leiden, bearing only the Chempedak and labelled by Thunberg "RADEMACHIA integra Thunb.," which was presumably part of the material sent to Houttuyn.

THE JACK. Thunberg showed that he had completely failed to perceive any difference between the Jack and the Chempedak in a paper published in 1779 with the title "*Sitodium incisum et macrocarpon, ususque fructuum qui exinde nascuntur, descripta a Carolo Petro Thunberg, M.D.*," in which he altered the generic name *Rademachia* (now spelling it more correctly as *Radermachia*) to *Sitodium* without giving either his reasons or any source for the name, although he had presumably obtained it from Banks, who communicated the paper to the Royal Society of London. The generic description (with *Soccus*, *Saccus*, *Radermachia*, and *Artocarpus* as synonyms) had only minor changes in wording and *Rademachia incisa* and *R. integra* were cited (in addition to the previous Rumphian names) under the two species, respectively, in synonymy. Therefore, although they are validly published here, the generic name *Sitodium* and the specific epithet *macrocarpon* must be rejected as nomenclaturally superfluous and thus illegitimate. Under *Sitodium macrocarpon*, Thunberg added to his previous Latin description of the Chempedak an account of the juvenile leaves and the fruit of the Jack (with a popular account of its uses in Ceylon, including recipes!). His paper renders illegitimate as a later homonym Gaertner's independent publication in 1788 of the generic name *Sitodium*, attributed by him to Banks. This was based on another description of the fruit of the Jack under the name *Sitodium cauliflorum*, but, as stated by Corner, the latter must also be regarded as a superfluous name for the Chempedak, since the author's intention, as indicated by the indirect citation of *Artocarpus integrifolia* ("*Artocarpus foliis integris*. LINN. [ed. Murray,] *syst. veg.* 838." [1784]) together with *Soccus arboreus* [sic] in synonymy, was to replace the earlier name, and this intention must be given

priority over the description and plates. Gaertner was the only author previous to Corner (l.c.) to describe and draw the female perianths (called by him "baccae partiales") as free below, though fused above.

Lamarck, in 1789, was the first post-Linnaean author to make a distinction between the Jack and the Chempedak, when he described in his "Encyclopédie Méthodique" three new species based on the Jack: *Artocarpus heterophyllus* (as *A. heterophylla*), with *Saccus arboreus major* as a synonym; *A. jaca*, which he recognized as close to the former, with Rheede's *Tsjaka-maram* among its synonyms; and *A. philippensis*. Under *Artocarpus jaca* he recognized a variety " β . *Eadem ramulis petiolis foliisque subhirsutis*," giving *Saccus arboreus minor*, *Artocarpus integrifolia* and *Rademachia integra* as synonyms. Unfortunately Lamarck's "illegitimate" action, while making this perfectly correct distinction, in thus subordinating the variety based on the earlier names and descriptions applicable to the Chempedak (of which he had seen no specimens) under his new species must, following Corner, make *Artocarpus jaca* yet another superfluous name for the Chempedak. The latter therefore, since no previous effective choice had been made between the two other simultaneously published names (for both of which Lamarck had mentioned the characteristic annulus at the base of the inflorescence head), took *A. heterophyllus* as the more appropriate, so that this becomes the correct name for the Jack. Examination in 1955 of the type material of the three species in the herbaria of Lamarck and de Jussieu (the latter including that of Commerson) at the Muséum National d'Histoire Naturelle, Paris, has confirmed that it consists solely of specimens of the Jack and that the species were based on somewhat marked differences in the leaves. Lamarck also included *Artocarpus incisus* (synonyms: *Soccus lanosus*, *S. granosus*, *Rademachia incisa*, "*Artocarpus* Forst.") in his account of the genus and described a fourth new species, *A. hirsutus* (as *A. hirsuta*), which he based entirely on Rheede's *Ansjeli*.

In spite of this distinction between the Chempedak and the Jack, the transference of the name *Artocarpus integrifolia* (with *Rademachia integra*) from the former to the latter was effectively achieved by Willdenow in 1805 in his edition of the "Species Plantarum" (the next work in which the genus was treated at all fully). He then "corrected" Lamarck's nomenclature, changing the name of his second species based on the Jack from *Artocarpus jaca* to *A. integrifolia*. He cited *A. jaca*, together with *Rademachia integra* and *Tsjaka-maram*, in synonymy, and recognized two varieties, " β . *ramulis petiolis, foliisque subtus hirsutis*" with *Saccus arboreus minor* as the only synonym, and " γ . *foliis indivisis trilobisve*" with *Artocarpus heterophylla* and *Saccus arboreus major* as synonyms.

POLYPHEMA. The description by Loureiro in 1790 of a new genus *Polyphema* to take the place of Linnaeus' *Artocarpus integrifolia* was due to a complete misunderstanding of the latter's generic description, which led Loureiro to suppose that it could only correspond to the first species, *Artocarpus incisus*, not seen by him, and to make several distinc-

tions between it and the plants he was studying which he felt justified their segregation as a new genus. Under this he described the Jack as *Polyphema jaca*, with *Saccus arboreus major* as a synonym, and the Chempedak as *P. champeden*, with *Saccus arboreus minor* as a synonym, and thus correctly separated the elements confused in *A. integrifolia* (though only in the synonymy). His description of the Jack appears to be entirely original (the type is in the British Museum (Natural History), London), but that of the Chempedak is largely based on Rumphius' account and it is doubtful whether he had ever seen a specimen. The plant is not found in Indochina in spite of his statement that it occurs in high woods there, and he may have been referring to a native species which he also used in making the description; the precise derivation of his account will be discussed further under *Artocarpus integer*.

Willdenow did not mention Loureiro's generic name, but in 1807 Sprengel made it the basis of an illegitimate name for the Chempedak, *Artocarpus polyphema*, under which this plant has been most widely known in the literature, although it was corrected to *A. champeden* in 1812 (by Stokes, Bot. Mat. Med. 4: 330; but universally ascribed to Sprengel, Syst. Veg. 3: 804. 1826).

HISTORY OF THE GENUS FROM 1807. A few other species were described in *Artocarpus*, but the first major contribution to the taxonomy of the genus was made by Trécul in 1847 in his paper on the Moraceae: Artocarpoideae and Conocephaloideae entitled "Mémoire sur la Famille des Artocarpées." He based his account mainly on the material then in the Muséum National d'Histoire Naturelle in Paris, and distinguished fifteen species, of which seven were new. In view of his limited material his work was very accurate and it is the only complete revision of the genus previously undertaken. He divided *Artocarpus* into two subgenera, *Jaca* (= subg. *Artocarpus*) ["*Perigonium* masculum diphyllum, foliolis plus minusve inter se cohaerentibus; *stipulae* duae oppositae, amplexicaules, altera marginibus alteram tegens; *folia* alterna"] and *Pseudojaca* ["*Perigonium* masculum tetra- rarissime triphyllum; *stipulae* 2 minimae, axillares vel sublaterales, non oppositae, nec amplexicaules; *folia* disticha"]. These subdivisions have been found to be well marked, although, as was pointed out by King (1889), the distinction based on the male perianth is not valid, since this is more variable within subgenus *Pseudojaca* than Trécul realized, even within the species studied by him. His use of the term opposite with respect to the stipules was a source of confusion to King, as shown by Renner (1907), since he restricted it to stipules having their midlines 180° apart.

In the years 1861 and 1867, Miquel published altogether 16 new species and combinations in *Artocarpus* (in addition to four that had appeared earlier), but many of the descriptions were based on poor material and it has only been possible to identify them by studying the types. More than one species was described under several different names and, although Miquel recognized Trécul's subgenera, he included in subg. *Artocarpus* a

species of *Sloetia* (Moroideae) and in subg. *Pseudojaca* one species (*A. limpato*) later transferred to *Prainea* and three which have been reduced to *Parartocarpus venenosus* (Zoll. et Mor.) Becc. (itself originally described as a species of *Artocarpus* in 1845).

The next important paper on the genus was King's monograph of 1889, "The species of *Artocarpus* indigenous to British India," in which he described seventeen species (seven of them and two varieties as new) known to him as native in India, Ceylon, Burma and Malaya. They were usually correctly defined (except for the two varieties), but, owing to his inability to study the types of Miquel and other authors, several of King's names must be replaced by earlier ones. He rejected Trécul's subgenera and arranged the species in two groups, in the first of which [the distal portions of] the "anthocarps"¹ were only partially united with each other so that the syncarp was spiny or tuberculate, while in the second they were completely united and the surface of the syncarp was smooth. Except for two new species included at the beginning of his first group (*Artocarpus forbesii* and *A. bracteata*) the subdivision does, however, correspond to Trécul's subgenera; this distinction between them happens to be fairly satisfactory in the species which King was considering, although, as was pointed out in the introductory paper, it does not hold for the entire genus. These two species should have been referred to *Parartocarpus* (in which the leaves are spirally arranged with non-amplexicaul stipules and the inflorescences are involucrate) and they represent the two other species which will be recognized in the genus. King did not mention *Parartocarpus*, and, although the description had been published in 1875, it may not have been available to him. The syncarps of these two species closely resemble those of some species of *Artocarpus* and King mistook the solid spinous process on the surface (the nature of which was discussed in the introductory paper) for tubular, perforate perianth apices. He did not consider leaf arrangement (explicitly at least), although his two groups differed in this respect also, and he rejected Trécul's perianth and stipular characters. The rejection of the stipular character was due to a double confusion: as already noted, King failed to comprehend Trécul's peculiar use of the term opposite; it has further been found in this study that he assigned a sterile specimen of *Artocarpus rigidus* to his *A. bracteata*, which caused him to describe the shoot as annulate, as it was in all the other species of his first group except *A. forbesii*, so that the stipular character would not give a "natural" classification, whereas the syncarp character apparently would. He considered that whether or not the stipules were amplexicaul depended merely on their size, and evidently attached no special significance to the occurrence of a basal involucre, which he observed only in *A. bracteata*.

In 1902 Beccari described nine new species and one new variety of *Artocarpus* from Borneo and New Guinea in an appendix to his "Nelle Foreste

¹ I.e., the female perianths; this term can, strictly, be applied only to those perianths enclosing mature seeds. It has not been used, since it would merely complicate the specific descriptions.

di Borneo," in which he also considered the characters in which *Prainea* and *Parartocarpus* differ from *Artocarpus*, though without fully clarifying them (see under *Prainea* above and *Parartocarpus* to follow), and removed King's two wrongly assigned species to *Parartocarpus*.

Finally, Renner, in a paper entitled "Beiträge zur Anatomie und Systematik der Artocarpeen und Conocephaleen, insbesondere der Gattung *Ficus*" published in 1907, discussed the systematy of the genera being studied, chiefly on the basis of their leaf anatomy, and, reinstating Trécul's subgenera, concluded that they, together with *Prainea*, should be treated as sections under *Artocarpus*. Renner's action in uniting *Prainea* with *Artocarpus* has been fully discussed in the introductory paper to this series and has been rejected, since the differences in leaf anatomy (and leaf arrangement) between the two subgenera (here maintained at this rank) could well have arisen by divergence from a common ancestor with the somewhat intermediate *Prainea*, whereas the unique syncarpium of *Artocarpus* indicates a close taxonomic relationship between the subgenera and contrasts markedly with the free female perianths of *Prainea*. Later authors have ignored both Renner's reduction of *Prainea* and Trécul's subgenera. Renner listed the anatomical characters for each of the species of *Artocarpus* available to him, citing the specimen(s) he had examined, but suggested no further taxonomic innovations, although his arrangement of the species follows a fairly "natural" order. The examination of leaf anatomy has been repeated for each of the species here recognized and details of the microscopic epidermal gland-hairs and of the hypodermis, if present, are given for each of the species in subg. *Artocarpus*, since their characters are of value in establishing the series.

Two purely taxonomic treatments should perhaps be mentioned, namely, Elmer's "Synopsis of *Artocarpus*" treating 16 species of the Philippines (1909), and Gagnepain's account of the genus in the "Flore Générale de l'Indochine" (1928) for which he described eight new species in 1926, several of which must be reduced.

There should also be added here a note on a paper which has only recently come to my notice, on the structure of the jackfruit, by D. D. Sundararaj and K. Ramanujam, "Studies on the floral morphology of Jack, *Artocarpus heterophyllus* Lamk. (Syn.: *A. integrifolius*, L.f.)," S. Indian Hort. 1: 56-61. figs. 1-12. 1953. These authors have described and illustrated the structure of the jackfruit at anthesis and maturity, and have emphasized, as was done in the introductory paper to this series, that the perianths are free below but fused above, in this species leaving the apices free, so that they have recognized three regions in each perianth. They have also pointed out again that, as had been made clear by Corner (Gard. Bull. Singapore 10: 56-81. 1939), the true fruits are enclosed by the free fleshy lower portions of the fruiting perianths. They describe the syncarp as a false fruit. However, they do not seem to have examined any very young female heads, in which the perianths would presumably be entirely free (as in *A. rigidus*, described in the introductory paper). They also state positively, but without bringing forward any evidence, that the an-

nulus represents the involucre bract of the inflorescence, whereas Corner had noted (l.c., 62, 76) that he had been unable to discover its morphological nature, although it was probably comparable to the bracts in *Parartocarpus*. This may well be the origin of the irregular row of bracts and the slight swelling of the top of the peduncle seen in some other species of *Artocarpus* but it is possible that the annulus represents a secondary enlargement of the latter.

GENDER OF ARTOCARPUS. Although the International Code of Botanical Nomenclature now states that *Artocarpus* must be treated as a masculine noun, since the Greek masculine noun *karpos* has been further altered to the masculine form in Latinization (Recommendation 75A), the genus has been considered as feminine by almost all previous authors except Linnaeus *filius* (1781), Renner (1907) and Corner (1939, 1940). The original specific epithet in *Artocarpus* — *communis* — was ambiguous in this respect, while Linnaeus *filius* treated his first species as masculine — *A. incisus* — but the second as feminine — *A. integrifolia*. Renner pointed out that this error probably arose in type-setting, since both the other species on the same page had feminine terminations, and he supposed that it had been perpetuated through the custom in Latin of treating all names of trees as feminine. In this revision only the original form in which a given name was published is indicated, if different from that now accepted (in addition to significant typographical errors).

CLASSIFICATION OF THE GENUS

The two subgenera of *Artocarpus*, established by Trécul in 1847, are here recognized on grounds which have already been fully discussed in the introductory paper in which they were also keyed out with the genera (p. 26, above). The characters distinguishing them, of which the vegetative are of more practical importance than the reproductive, may be summarized as follows: in subg. *Artocarpus* the leaves are spirally arranged with large, amplexicaul stipules leaving annulate scars and they have a long-armed, usually very loose spongy mesophyll with ellipsoid to globose resin-cells, and epidermal gland-hairs with a 4–16-celled head, whereas in subg. *Pseudojaca* the leaves are alternate and distichous with small non-amplexicaul stipules leaving lateral or partially intrapetiolar scars, the mesophyll is compact, and the heads of the gland-hairs are usually unicellular. The syncarp in subg. *Pseudojaca* is globose or somewhat lobed with a fleshy, smooth or papillate surface, while in subg. *Artocarpus* both shape and surface are variable, though the syncarp usually bears distinct indurated or fleshy processes, or, where it is smooth or nearly so, it is ellipsoid to cylindrical.

While the species in this genus are, on the whole, distinct and readily separable, this is not always the case with the subdivisions between the level of the subgenus and the species. There is also a marked contrast

in the range of variation exhibited within the two subgenera and this is reflected in the classification here suggested for the species within them. In subgenus *Artocarpus* there is a wide range of variation — within the fairly strict limits imposed by the structure — in the syncarps (especially in the shape, length, consistency and indumentum of the processes) and the species can be recognized on the differences in these alone, although they are supported by more or less marked differences in the male inflorescences (in shape, size and surface, and in peduncle indumentum and length) and in the shoot (in indumentum and leaf size and shape). The pattern of variation warrants the creation of two sections with two and four series, respectively, the basis for which will be discussed below.

In subgenus *Pseudojaca*, on the other hand, while two sections will also be created, one is for an anomalous species, *Artocarpus altissimus*, and the other presents little variation between the species. The inflorescences are so reduced that the entire male and female heads provide the unit of variation in establishing the species. The heads of different species vary in size and shape, in the length and indumentum of the peduncle, and, in the female head, in the appearance of the surface at anthesis and maturity, its indumentum, the degree of exertion of the styles, and whether or not the interfloral bracts persist or lobing develops. There are also vegetative differences between the species — in shape, size, prominence of venation, petiole length and indumentum of the leaf — but, while most species can, with practice, be identified when sterile, the differences are often not readily definable. As might be expected where there are limited possibilities for variation, parallel evolution has occurred, especially in the vegetative characters, and the species may only be definable by using a combination of characters. The only discontinuous “morphological” variation occurring in this section is in the shape of the interfloral bracts, which is used to separate three species as one series of limited geographical distribution, leaving the remainder as a large group which is probably best treated as a single series. Although subsidiary groups can be recognized within the latter, the definitions necessary for these are somewhat complex, and there are also several species showing reticulate relationships, and a few of which the alliances are doubtful.

In the keys to both subgenera proportions have been used — length to breadth of inflorescence head in subg. *Artocarpus*, and length of head to length of peduncle in subg. *Pseudojaca*. These recognize and utilize characteristic differences between species groups in the shape of the head or in the relative length of head and peduncle. These differences hold, with a few exceptions, for both male and female inflorescences, thus making possible the construction of a “natural” key which can be used (at this dichotomy at least) at any stage in the development of the inflorescence, since the relationships remain fairly constant throughout its growth. The use of these ratios also allows for the considerable variation in size, rather than shape, which may occur in the inflorescences, depending largely on the part of the plant on which they are borne. There are some species, especially in subg. *Pseudojaca*, where these relationships do not

always hold, but they are relatively few in number and have been allowed for as far as possible.

ECOLOGICAL AND BIOLOGICAL NOTES

The species of *Artocarpus*, except for a few belonging to subg. *Pseudojaca*, are large trees of the high forest and are mainly restricted to evergreen forest in the tropical everwet zone or in areas with a relatively mild monsoon climate. They are usually found below an altitude of 3000 ft., though several species may occur up to 5000 ft. One species, *Artocarpus communis*, is abundant in swamp forest in New Guinea, and others are recorded from swampy areas or from the banks of streams. The majority of the species in everwet forest are themselves evergreen, although they may, especially in subg. *Pseudojaca*, show marked flushes of new growth, but *Artocarpus dadah* is deciduous. Of the species restricted to regions with monsoon climate some, including *A. lakoocha*, are deciduous, but others, such as *A. gomezianus*, are evergreen. The latter (as ssp. *gomezianus*) is the only entity within the genus to show a marked climatic discontinuity — between Lower Burma and Siam, and central and eastern Java. *Artocarpus lakoocha*, which is the most wide-ranging species on the continent of Asia, is also the most tolerant of cool temperatures and low rainfall, although it is damaged by frost.

In considering biological aspects of the variation in growth habit and in the syncarp in this genus several more or less parallel trends may be distinguished. The first tendency is shown in the arrangement of the leaves, which in subg. *Artocarpus* are borne spirally on usually ascending twigs, whereas the ultimate shoots in subg. *Pseudojaca*, with their alternate and distichous leaves form more or less applanate sprays of foliage. Associated with the latter habit is a general reduction in massiveness, but within each subgenus there are also tendencies to reduction in the size of parts, culminating in subg. *Artocarpus* in *A. kemando*, and in subg. *Pseudojaca* in *A. styracifolius*.

There is in subgenus *Artocarpus* considerable variation in the form of the adult leaves, which are pinnate in *A. anisophyllus* (though unusual in not disarticulating when they fall) and pinnatifid in *A. communis* and its allies, all these species having very stout twigs. In the saplings of several species the leaves are very large and highly dissected (twice or thrice pinnatifid and to six feet in length in *A. elasticus*). Members of this subgenus were mentioned by Corner in his exposition of the "Durian Theory" (Ann. Bot. II. 13: 367–414. 1949) as showing in their sapling and adult stages the transition from a "pachycaul" habit, with a sparingly branched trunk and large, compound leaves, to the modern "leptocaul" tree, with slender twigs and horizontal sprays of simple leaves. They were also noted as exhibiting the principle of "axial conformity" or correspondence between the massiveness of the axis and the size and complexity of its appendages, which may be extended through *A. anisophyllus* and *A. communis* to the most slenderly constructed species of both subgenera. Except in two cauliflorous species

of subg. *Artocarpus* (*A. integer* and *A. heterophyllus*) there is a general correspondence throughout the genus between the size of the twigs and leaves and that of the syncarps, which are borne with the male inflorescences among the foliage (although before they mature the subtending leaves may have fallen). A different trend was pointed out by Corner in *A. heterophyllus*, in which the twigs were slender with simple leaves, tending to form an appanate spray (cf. subg. *Pseudojaca*), while the enormous syncarp was borne on the trunk or large branches, a necessary development if the massive fruit was to be retained.

The syncarps within the genus also vary between two types of organization, namely, those in which each seed is surrounded by a pulpy perianth and the rest of the syncarp is more or less fibrous or indurated, and those in which the entire syncarp is soft and fleshy but the fruiting perianths are not markedly hypertrophied. The first type is best developed in the armoured syncarps of the first section of subgenus *Artocarpus* (which includes *A. rigidus*), and the second is found in the small, nearly smooth syncarps of *A. kemando* and its allies, and of subg. *Pseudojaca*. The remaining species in subg. *Artocarpus* have small to fairly large, moderately fleshy syncarps, usually with well developed firm, or fleshy and often flexuous processes on the surface. They lack (so far as evidence is available) conspicuously enlarged fruiting perianths, except in the very large syncarps of the two cauliflorous species. However, the perianths in *A. elasticus* and *A. sericicarpus* are apparently somewhat pulpy. In the species with an armoured syncarp and also in a number of species in subg. *Pseudojaca* the seeds are enclosed in more or less well differentiated horny endocarps which may become free by the decay of the rest of the pericarp, while in other species of subg. *Artocarpus* the entire pericarp is indurated. This protection is lacking in the cauliflorous species, but in *A. heterophyllus* there is a horny outer testa.

In spite of the varying nature of the attractive element in the syncarp of *Artocarpus* the mode of dispersal is much the same throughout the genus, which is primarily adapted for distribution by arboreal mammals, although the smaller fruits of subg. *Pseudojaca*, many of which are yellow, red or purple, may also be eaten by birds. (Troup (Silvicult. Ind. Trees 3: 884. 1921) records that the fruit of *A. lakoocha* is eaten by parrots and minahs, and also by monkeys.) The larger fruits in the genus, according to Ridley (The Dispersal of Plants. 1930), are bitten to pieces on the tree by monkeys, squirrels and civet-cats. He describes how the orange syncarps of *Artocarpus rigidus* (for which the English name is the Monkey Jack) are eaten in Malaya by a macaque monkey, which readily tears apart the spiny covering to reach the edible sweet orange pulp surrounding the seeds, and how as much fruit may be thrown away as is eaten. It is presumably by means of this wastage of portions of the fruit, which are let fall by the animals eating them, that the seeds are more widely dispersed, but they will, in any case, germinate in syncarps which fall to the ground from the tree. Ridley suggests that the enormous syncarps borne on the trunk in *A. integer* (and presumably also in *A. heterophyllus*) are eaten

by forest ungulates, such as wild cattle, pigs and elephants, which can easily reach them. It should be noted that the seeds in this genus have no period of dormancy, but germinate immediately, and that they are unable to withstand dessication.

The mode of pollination in *Artocarpus* is variable. Corner (Wayside Trees, 650. 1940) recorded that male heads in *A. heterophyllus*, *A. integer* and *A. dadah* had a sweet scent of honey and burnt sugar, attracting small flies and beetles, which were the pollinating agents, but that *A. rigidus*, *A. communis* and *A. elasticus* were apparently wind-pollinated, since the male heads had no scent, but gave off clouds of pollen when they were moved. Van der Pijl (Ann. Bogor. 1:79–82. 1953) studied pollination in *Artocarpus heterophyllus* and found that the anthers emerged over a period of some days and produced a sticky pollen. The flies bred on the decaying flower-heads which had fallen from the tree and thus established a brief symbiotic relationship with the plant during the period of anthesis.

Subgenus *Artocarpus*

Artocarpus subgenus *Jaca* Trécul, Ann. Sci. Nat. Bot. III. 8: 110. 1847.

Artocarpus section *Jaca* Renner, Bot. Jahrb. 39: 363. 1907.

Leaves spirally arranged, simple and entire to pinnatifid, or pinnate (*A. anisophyllus*); gland-hairs superficial to deeply sunken, heads 4–16-celled; spongy mesophyll long-armed and usually very loose, with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*). *Stipules* large, intra-petiolar, amplexicaul, scars annulate. *Inflorescences* with or without sterile, solid, elongate perianths. *Male head*, perianths tubular, shallowly (rarely deeply) 2(–3)-lobed above, or perforate. *Syncarp* globose or subglobose, covered by indurated processes, or ellipsoid to cylindrical, varying subglobose, covered by firm or flexuous processes or less commonly areolate.

This subgenus is divided into two sections, *Duricarpus* and *Artocarpus*, based on the shape of the inflorescence heads and the presence or size of the interfloral bracts, on various characters of the syncarps, and, less certainly, on the mode of germination; but there are also three anomalous species which will be discussed below. The first section is a fairly homogeneous group of seven species, characterized primarily by the syncarp which has the surface armoured (whence its name) by the indurated free apices of the perianths. The free proximal region of those perianths that form seeds becomes fleshy, and encloses an ovary having a terminal style and developing a more or less clearly differentiated horny endocarp (becoming free by the decay of the rest of the pericarp in *A. anisophyllus* and *A. lanceifolius*). The embryo is symmetrical with a minute apical radicle and the appressed faces of the cotyledons at an angle of 30–90° to the median plane. The syncarp is globose or nearly so, and the male head varies from globose to cylindrical or clavate, but is never more than three and one half (rarely four) times as long as broad. In both there

are conspicuous peltate interfloral bracts, but these are mostly lost from the syncarp at or before anthesis, although a few frequently persist. The mode of germination is known in several species and the first pair of leaves subsequent to the cotyledons is consistently opposite, though later leaves are spirally arranged. For comparison with the series of the next section, it may be noted that a hypodermis is present in the leaves of only two species and that it consists of cells which are elongate in surface view, while the gland-hairs have a globose, 4-16-celled head. On the basis of the leaf characters, together with a difference in the shape of the male heads, two species are separated as series *Laevifolii*, leaving the rest in series *Asperifolii*.

The second section, *Artocarpus*, is larger and more heterogeneous, but the species are united and are distinguished from sect. *Duricarpus* by their more or less elongate inflorescences, the absence or small size of the interfloral bracts and the fleshy syncarp with the fruiting perianths becoming markedly fleshy in only two species, and the mature ovaries with a lateral or sub-basal style and no clearly differentiated endocarp (so far as the internal structure is known; exceptions presented by the anomalous species will be noted below). The contrast in the shape of the inflorescences is more marked in the male head which is usually at least four times as long as broad (though as little as one and one half times in *A. heterophyllus*). The syncarp is, however, usually ellipsoid to cylindrical and only rarely subglobose, and the surface is either covered by firm, or more or less fleshy and often flexuous processes of varying shape or, less commonly, merely areolate. Interfloral bracts are frequently entirely lacking and, when present, they are scattered and inconspicuous, with small heads to 0.2 mm. across. The position of the style, though variable, is always at least one third of the way down the ventral face of the ovary at maturity, and the radicle is likewise ventral, so that the long axis of the embryo is oblique. The appressed faces of the cotyledons lie either in the median plane of the ovary, in which case the embryo is usually symmetrical, or they are also more or less oblique, with the uppermost cotyledon frequently reduced in size. Details of germination are known for only four species (*A. communis*, *A. integer*, *A. heterophyllus* and *A. elasticus*) but the first leaves appear to be always spirally arranged, except, perhaps, in *A. communis*, and to be preceded by scale leaves.

The classification of the species within section *Artocarpus* has presented some problems, in addition to those originating in the three species that have been separated as anomalous. It has been concluded that four series should be recognized and these are based, as in sect. *Duricarpus*, primarily on characters of the leaves, namely the shape of the gland-hairs, and the presence or absence of a hypodermis and of resin-cells. However, with one exception, each is further distinguished by characters that are unique to it. Series *Rugosi*, with seven species, is readily distinguished by the anatomical characters of the leaves, which have a continuous hypodermis of isodiametric cells and gland-hairs with a depressed-globose, 4-celled head, and by the variously ridged surface of the male head, from which it receives its name.

In the other species of the section the surface of the male inflorescence is smooth (except occasionally in *A. integer*) and an irregular hypodermis is found only in some specimens of *A. blancoi*. Series *Incisifolii*, with six species, is also well distinguished by the flattened, peltate, 8(-16)-celled heads of the gland-hairs, the frequently pinnatifid adult leaves, the inflated hairs usually covering the syncarp processes and male perianth lobes, and the relatively large size of the anthers, which range from 0.3-1.5 mm. in length (in no other species of the subgenus do they exceed 0.5 mm.). The remaining series, *Cauliflori* and *Angusticarpi*, each with two species, have entire adult leaves with gland-hairs having a depressed-globose, 6-10-celled head and consistently slender twigs, as compared with series *Incisifolii*. Series *Cauliflori* is distinguished from series *Angusticarpi* (and all other species of the subgenus) by the very large syncarps borne on the branches and trunk, with markedly hypertrophied fleshy fruiting perianths, the absence of resin-cells from the leaves, and possibly also by the germination of the seed, in the course of which the two cotyledons separate to allow the emergence of the plumule. Although the cauliflorous syncarp of these species gives them a very distinctive appearance, the characters just listed do not appear to be of sufficient importance to justify separating this series from the rest in the section. Series *Angusticarpi* thus remains as an unspecialized, though generally reduced, group which does not show clear alliances with any other series. The appearance of the leaves is quite distinct from that of series *Cauliflori*, as may be seen from the key to the subgenus. The value of the syncarp in classifying this section, although considerable in distinguishing the species, is limited at the level of the series, since there has been parallel evolution in the development of sterile perianths forming elongate, solid processes on the surface in one or more species of all series except *Cauliflori*: in series *Incisifolii* and *Angusticarpi* there may also be similar perianths in the male inflorescence. While the embryos may well provide characters distinguishing the series — those of series *Incisifolii* have relatively well developed cotyledonary stalks and radicles and the entire pericarp wall is indurated — they are very variable from species to species and evidence is unfortunately insufficient to determine their taxonomic value. Details are given for each species in the section when available.

The validity of these groups is supported by their geographical distribution. Section *Duricarpus* and series *Rugosi* are both centred in western Malaysia (Malaya, Sumatra, Borneo, Java) and the former occurs northward to Sikkim and Indochina, and is perhaps represented by indigenous species in the Philippines, while the latter has one species reaching southern Tenasserim and Palawan, and another extending through the Philippines, to Celebes and the Moluccas. Series *Incisifolii*, on the other hand, has species in the Philippines, the Moluccas and New Guinea (and perhaps Melanesia if *Artocarpus communis* is indigenous there). The most widespread groups are series *Cauliflori* and *Angusticarpi*. The first has one species (*A. integer*) extending from western New Guinea to Malaya and reaching peninsular Burma and Siam, although it is absent from the Philippines.

and another (*A. heterophyllus*) perhaps indigenous in peninsular India. The second has one species in Malaya and Sumatra, and one with a distribution similar to that of *A. integer* but extending to the Nicobar Islands instead of north of the Malayan border.

On the basis, primarily, of the shape of the inflorescence heads, three species, which are otherwise anomalous in that each is, in various characters, intermediate between the sections, are placed at the end of sect. *Artocarpus*. Owing to this intermediacy and the fact that the structure of the mature syncarp is known in only one of them, they are not assigned to any of the series here established. Although a separate series should, perhaps, be created for each one of them, this is deferred, pending a more complete knowledge of the syncarps.

Of these species, *Artocarpus hirsutus*, from peninsular India, has an exceptionally long and slender male inflorescence indicating an affinity with sect. *Artocarpus*, but a subglobose to shortly cylindrical syncarp covered by indurated, narrowly cylindrical processes, which is somewhat similar to the syncarps of sect. *Duricarpus*. From the account given in Troup (*Silvicult. Indian Trees* 3: 876. fig. 323. 1921) it is evident that the mode of germination is also the same as that found in sect. *Duricarpus*. The characters of the perianth and ovary do not, however, appear to be in agreement. The internal structure of the mature syncarp is not known, but the submature fruiting perianths are thin and the ovary is membranous with a subapical style. In view of these differences, together with the shape of the male head and the complete absence of bracts from the inflorescences (although this last character may have arisen by parallel evolution), this species is assigned to sect. *Artocarpus*. The induration of the syncarp processes is assumed to be of less taxonomic importance, although it provides, together with the hispid twigs and the appearance of the leaves (the gland-hairs have a depressed-globose, c. 6-celled head), a superficial resemblance to *A. rigidus*.

The two other species, *Artocarpus nobilis* and *A. sepicanus*, are remarkable in that, although one comes from Ceylon and the other from New Guinea, they share the characters of narrowly cylindrical inflorescences (cf. sect. *Artocarpus*) and well developed, peltate interfloral bracts (cf. sect. *Duricarpus*) which are persistent and conspicuous on the syncarps. In other respects, however, the appearance of the syncarps is very different: in *A. nobilis* the surface is covered by short, umbonate, indurated processes, while in *A. sepicanus* the syncarp is fleshy, with a pubescent, apparently completely smooth surface (cf. species of subg. *Pseudojaca*) and the styles are exerted through perforations in this. The internal structure is known only in *A. nobilis*, in which the fruiting perianths are thin, the ovary is pergamentaceous with a subapical style, and the symmetrical embryo lies obliquely in the median plane of the ovary with the relatively large radicle ventral (cf. series *Incisifolii*), although in its germination, as in *A. hirsutus*, the first pair of leaves is opposite. *A. nobilis* also shows an alliance with series *Incisifolii* in the shape of the gland-hairs, which have a peltate, flattened, 8-celled head, but in *A. sepicanus* the gland-hairs, which are

unusual in being deciduous at a very early stage, have a globose, 6–8-celled head.

These three species and, more especially, the curious resemblances between *A. nobilis* and *A. sepicanus* are a reminder of the long evolutionary history that can be assumed for this genus. It would appear that they are “relicts”, and the persistence of a few such species that do not readily fit into a classification intended to reflect the affinities of the groups dominant today is scarcely surprising.

The series recognized within section *Artocarpus* are not, however, necessarily closely allied and it is not suggested that any one of them is directly ancestral to the others. Section *Duricarpus* may represent either an offshoot from sect. *Artocarpus* or an independent line of evolution within the genus. The anomalous species, as has already been implied, are probably the remnants of a wider variation exhibited by the genus in the past, and this may also be true of series *Cauliflori*.

KEY TO THE SPECIES OF ARTOCARPUS SUBGENUS ARTOCARPUS

1. Male head globose to clavate or short-cylindric, length/breadth = 1–3.5(–4), the surface largely covered by the peltate heads of numerous bracts; syncarp subglobose, length/breadth = 1–1.5, the surface covered by indurated processes; adult leaves pinnate or entire (rarely trilobed above the middle), the latter usually with fewer than 20 intercostals.²
 2. Syncarp processes narrowly cylindric, 5–8 × 1 mm., hispid, peduncle 4.5–6.5 cm. (male head narrowly cylindric, 7–16 × 0.5–0.7 cm.). Southern India. 25. *A. hirsutus*.
 2. Syncarp not as above. Sect. DURICARPUS.
 3. Twigs and leaves glabrous; male head ellipsoid to short-cylindric; syncarp processes glabrous or pubescent. Series LAEVIFOLII.
 4. Leaves pinnate; syncarp processes elongate, narrowly cylindric, 6–8 × 1–1.5 mm., glabrous. Malaya, Sumatra, Borneo. 1. *A. anisophyllus*.
 4. Leaves simple; syncarp processes short, broadly cylindric, truncate, c. 3.5 × 3 mm., and surface hence tessellate, or slightly tapering, obtuse, c. 1.5 × 1.5 mm., and somewhat separated, appressed-pubescent. Malaya, Sumatra, Borneo. 2. *A. lanceifolius*.
 3. Twigs and leaves (at least on the main veins beneath) hispid or hispid-pubescent; male head globose to obovoid or clavate; syncarp processes hispid. Series ASPERIFOLII.
 5. Syncarp processes broadly cylindric, 1.5–3.5 mm. long.
 6. Leaves smooth above, hispid-pubescent on the main veins only beneath; male peduncle 1–5 × 0.3 cm.; syncarp processes hispid from patent, usually slightly crisped hairs. Indochina, British North Borneo. 3. *A. melinoxylus*.
 6. Leaves scabrid above, hispid-pubescent throughout beneath; male peduncle 6–7.5 × c. 0.15 cm.; syncarp processes hispid from appressed hairs. Northeastern India, Burma, Andaman and Nicobar Is. 4. *A. chaplasha*.

² The intercostal veins should be counted along the distal side of a lateral vein near the middle of the leaf.

5. Syncarp processes elongate, 5–13 mm. long, narrowly cylindrical with clavate tips, or tapering.
7. Leaves hispid-pubescent above; male head 4–9 × 2.5–3.5 cm., peduncle 2.5–7 cm.; syncarp processes narrowly cylindrical with clavate tips, 8–13 × 1 mm. Borneo, Philippines. 5. *A. odoratissimus*.
7. Leaves becoming smooth or scabrid above; male head to 3 × 2 cm., peduncle to 3 cm.; syncarp processes tapering, 5–9 × 1–1.5 mm.
8. Twigs and peduncles patent-hispid; male peduncle 1.2–3 cm. Malaya. 6. *A. hispidus*.
8. Twigs and peduncles appressed-hispid; male peduncle 0.2–0.6 cm. Indochina, southern Burma and Siam, Malaya, Sumatra, Borneo, Java. 7. *A. rigidus*.
1. Male head cylindrical, varying ellipsoid or clavate, length/breadth = (1.5–) 4–20, bracts usually very few or entirely lacking; syncarp ellipsoid to cylindrical, varying to subglobose, length/breadth = 1–4, the surface covered by more or less fleshy, firm or flexuous processes (indurated in *A. nobilis* and *A. hirsutus*), varying to areolate or smooth; adult leaves pinnatifid to entire, the latter frequently with more than 20 intercostals. Sect. ARTOCARPUS.
9. Inflorescences narrowly cylindrical, the surface entirely or partly covered by the peltate heads of numerous bracts, persistent in both sexes.
10. Twigs 10–12 mm. thick; leaves frequently distinctly and regularly crenate between the lateral veins; male head 7–13 × c. 1.5 cm.; syncarp to 20 × 10 cm., processes short-cylindrical, obtuse, 1 × 1–1.5 cm., indurated. Ceylon. 26. *A. nobilis*.
10. Twigs 3–5 mm. thick; leaves not as above; male head to c. 3 × 0.5 cm.; syncarp to c. 4.5 × 1.5 cm., fleshy, surface (?) smooth, pubescent. New Guinea. 27. *A. sepicanus*.
9. Inflorescences not as above.
11. Twigs appressed-hispid; male head narrowly cylindrical, 7–16 × 0.5–0.7 cm.; syncarp to c. 5 × 4 cm., processes narrowly cylindrical, 5–8 × 1 mm., rigid, hispid. Southern India. 25. *A. hirsutus*.
11. Male head not as above, *or* twigs subglabrous; syncarp not as above.
12. Male head with the surface smooth; twigs glabrous, *or* villous from greyish, varying pale rufous hairs, *or* pilose or pungent from patent rufous hairs.
13. Twigs (4–)6–22 mm. thick, villous, varying glabrous or with patent acicular hairs; adult leaves entire or pinnatifid; male head 1–30 × 0.7–3(–5.5) cm.; syncarp processes rough from the apices of deflexed, inflated hairs (except in *A. communis* and sometimes *A. horridus*), styles bifid or simple. Series INCISIFOLII.
14. Adult leaves entire or pinnatifid, with up to 5(–9) pairs lateral lobes; inflorescences with all the flowers fertile; anthers 0.3–0.8 mm. long.
15. Adult leaves becoming entire; syncarp less than 10 cm. across, the processes (and the perianth lobes in the male head) rough from the apices of deflexed, inflated hairs *and/or* the twigs with rigid, patent, acicular hairs.

16. Twigs villous to glabrous; syncarp processes never glabrous.
17. Male head 10–21 × 1.3–2 cm., anthers 0.7 mm. long; syncarp processes 8–15 × 1.5 mm.; inflorescences usually with scattered bracts. Mindoro, Luzon.
..... 8. *A. blancoi*.
17. Male head 1–17 × c. 0.7 cm., anthers 0.3–0.5 mm. long; syncarp processes 2.5–4 × 2.5–3 mm.; inflorescences without bracts. Philippines. 9. *A. treculianus*.
16. Twigs with rigid, patent, acicular hairs, c. 2 mm. long; syncarp processes c. 3 × 1.5–3 mm., varying glabrous. Moluccas.
..... 10. *A. horridus*.
15. Adult leaves generally pinnatifid; syncarp more than 10 cm. across, the processes or facets (and the perianth lobes in the male head) with slender, patent hairs or glabrous (neither inflated nor acicular hairs present). 11. *A. communis*.
14. Adult leaves deeply pinnatifid, with 7–20 pairs of lateral lobes; inflorescences often with solid, sterile, elongate flowers; anthers 1.2–1.5 mm. long.
18. Lobes of leaf 12–20 pairs; male head with a few solid, cylindric perianths projecting to 0.5 mm. from the surface; syncarp processes all 3 × 2 mm., perforate, styles simple. Luzon.
..... 12. *A. pinnatisectus*.
18. Lobes of leaf 7–10 pairs; male head with numerous solid, cylindric perianths with clavate tips projecting to c. 2 mm. from the surface; syncarp processes of two lengths, 15 × 1 mm., solid, and 5 × 1 mm., perforate, styles bifid. Samar, Mindanao.³
..... 13. *A. multifidus*.
13. Twigs 2–6 mm. thick, glabrous or pilose from patent, rufous hairs; adult leaves entire; male head 2–7.5 × 0.5–1.2 (–3) cm.; syncarp processes puberulent or minutely hispid, styles simple.
19. Cauliflorous or ramiflorous; leaves with the lateral veins curved, 6–10 pairs; syncarp 15–100 × 10–50 cm., fruiting perianths markedly fleshy. Series CAULIFLORI.
20. Twigs and peduncles usually pilose from patent, rufous hairs, c. 3 mm. long; base of leaf abrupt, intercostals to c. 10; inflorescences without a basal annulus. 14. *A. integer*.
20. Twigs and peduncles glabrous; base of leaf decurrent, intercostals c. 10–14; inflorescences with a

³ The distribution of series *Incisifolii* within the Philippines is given as a rough guide only; the less common species will probably be found to occur more widely.

basal annulus formed by the enlargement of the top of the peduncle into a narrow flange.

- 15. *A. heterophyllus*.
19. Not cauliflorous or ramiflorous; leaves with the lateral veins straight; syncarps 6.5–8.5 × 2–3.5 cm., fruiting perianths not fleshy. Series ANGUSTICARPI.
21. Leaves elliptic, lateral veins 11–16 pairs; male head without elongate solid perianths; syncarp with processes all perforate, conical and up to 1.5 mm. long, or the apices depressed and the surface hence areolate. Malaya, Sumatra. 16. *A. lowii*.
21. Leaves ovate to ovate-elliptic, lateral veins 6–12 pairs; male head with filiform solid perianths projecting to 1 mm. from the surface; syncarp with processes mostly perforate, conical, to 1.5 mm. long, but a few solid, attenuate, to 4 mm. long. Nicobar Is., Malaya, Sumatra, Borneo, Celebes, Moluccas, New Guinea. 17. *A. teysmannii*.
12. Male head with the surface variously rugose; twigs hispid, hispid-pubescent or villous, the hairs usually rufous. Series RUGOSI.
22. Shoots large to massive: twigs 5–20 mm. thick; male head 6–20 × 1–2.5 cm., the peduncle 3.5–10 cm.; syncarp 8–12 × 5–5.5 cm., usually with solid, flexuous processes, the peduncle 5.5–18 cm.
23. Leaves with 11–16 pairs lateral veins; male head with the surface rugose-sulcate, not pilose; flexuous syncarp processes with short, patent, or long, appressed hairs.
24. Twigs hispid, varying subglabrous; leaves thickly coriaceous; male head rugose-sulcate, perianths without crisped hairs; flexuous syncarp processes to 18 × 1.5 mm., shortly hispid, or none.
25. Leaves smooth above, or nearly so; male head 6.5–10.5 × 1 cm.; syncarp with all processes c. 3 × 2 mm., or a few slightly elongate. Malaya, Sumatra. 18. *A. scortechinii*.
25. Leaves scabrid above; male head 6–15 × 1.5–2.5 cm.; syncarp with flexuous processes 10–18 × 1–1.5 mm., shortly hispid. Peninsular Burma and Siam, Malaya, Sumatra, Borneo, Java, Lesser Sunda Is., Palawan. 19. *A. elasticus*.
24. Twigs (often sparsely) villous; leaves coriaceous; male heads rugose or sub-tuberculate, perianths with crisped hairs; flexuous syncarp processes 20–35 × 0.5–1 mm., subappressed-pubescent, hairs to 2 mm. long. Borneo, Philippines, Celebes, Moluccas. 20. *A. sericicarpus*.
23. Leaves with 15–23 pairs lateral veins; male head with the surface tuberculate from obtuse processes, c. 3 ×

- 2 mm., the apices pilose, hairs rufous, to 2 mm. long; flexuous syncarp processes to 10×0.5 mm., scabrid from recurved hairs. Borneo. 21. *A. tamaran*.
22. Shoots smaller: twigs 2–3 mm. thick; male head $2-5.5 \times 0.3-0.6$ cm., the peduncle 0.5–2 cm.; syncarp $4-4.5 \times 2-2.5$ cm., without sterile processes, the peduncle 0.5–4 cm.
26. Leaves subappressed-pubescent throughout beneath; male peduncle c. 2 cm.; syncarp with acute conical processes. Sumatra. 22. *A. sumatranus*.
26. Leaves usually appressed-pubescent on main veins only beneath; male peduncle to 1.3 cm.; syncarp with low, obtuse or truncate processes, or nearly smooth, the surface areolate.
27. Leaves elliptic-oblong varying elliptic, acute to acuminate, glabrous above; peduncles patent-pubescent, in male 0.7–1.3 cm., in female 1.5–4 cm.; syncarp pubescent, with low, obtuse processes, or nearly smooth, the surface areolate. Malaya, Sumatra, Borneo. 23. *A. kemando*.
27. Leaves obovate-elliptic varying elliptic, shortly and obtusely acuminate to retuse, young leaves appressed-puberulent above; peduncles velutinous, in male c. 0.5 mm., in female 0.3–0.8 cm.; syncarp velutinous, tessellate from very low, truncate, processes. Malaya, Sumatra. 24. *A. maingayi*.

Artificial keys for the identification of specimens bearing either male or female inflorescences are provided at the end of the treatment of this subgenus, and the second of these is illustrated.

Section *Duricarpus* Jarrett, sect. nov.

Folia adulta pinnata (*A. anisophyllus*) vel simplicia, integra, juvenilia pinnatifida; hypodermis absens, vel imperfectum, cellis elongatis compositum. *Inflorescentiae* bracteis interfloralibus peltatis, syncarpio subdeciduis. *Capitula mascula* subglobosa, obovoidea, clavata, ellipsoidea vel breviter cylindrica. *Syncarpia* globosa, vel subglobosa, processibus induratis oblecta; ovaria stylis terminalibus; semina testis pergamentaceis, rubris, pericarpis induratis, perianthis carnosisque inclusa; embryum in longitudinem positum, cotyledonibus aequalibus, radícula supera.

TYPE SPECIES: *Artocarpus rigidus* Blume.

Although the distinctive feature of this section is the syncarp, there is considerable variation in its appearance due to the differing shapes of the indurated processes (free perianth apices) covering it, which may be either narrowly cylindrical (*A. anisophyllus* and *A. odoratissimus*, with clavate tips in the latter), or tapering so that the syncarp is echinate (*A. hispidus*, *A. rigidus*), or short and obtuse or truncate so that the surface is more or less clearly tessellated (*A. lanceifolius*, *A. melinoxylus*, *A. chaplasha*). Other characters, however, suggest that these resemblances do not neces-

sarily indicate the closest relationships of the species. *Artocarpus anisophyllus* stands out by reason of its pinnate leaves, but in the presence of a hypodermis, the deeply sunken gland-hairs, and the glabrous shoot, a close affinity is shown with *A. lanceifolius*, which is confirmed by the ellipsoid to cylindrical male inflorescences, and the strongly differentiated endocarp. *Artocarpus odoratissimus*, *A. hispidus* and *A. rigidus* are likewise united by their obovoid, subglobose or clavate male inflorescences, the elongate, hispid syncarp processes, and the hispid shoots. Between them may be placed *A. melinoxylus* and *A. chaplasha*, which resemble the latter group in the characters of the shoot and the male inflorescence, but *A. lanceifolius* in the surface of the syncarp. These are the only two species in the section of which the distinctness is in any doubt, and the characters separating them are listed under *A. melinoxylus*. As noted above, two series are distinguished on the basis of leaf anatomy, indumentum of the shoot and shape of the male head, of which the first, series *Laevifolii*, includes *Artocarpus anisophyllus* and *A. lanceifolius*, while the rest of the species are placed in series *Asperifolii*.

Series *Laevifolii* Jarrett, ser. nov.

Ramuli et folia subglabri; folia hypoderme imperfecto, cellis elongatis composito, glandulis profunde immersis, capitibus globosis, 4–6-cellis; inflorescentiae masculae breviter ellipsoideae vel subcylindricae.

TYPE SPECIES: *Artocarpus anisophyllus* Miq.

1. ***Artocarpus anisophyllus*** Miq. Fl. Ind. Bat. Suppl. 422. 1861, "*anisophylla*;" Renner, Bot. Jahrb. 39: 366. 1907; Merr. Pl. Elmer. Born. 45. 1929; Corner, Wayside Trees, 652. t. 191, 192. 1940. Holotype, Sumatra, *Teysmann HB 3698* (U); isotypes (BO, K, L).

Artocarpus klidang Boerl. Handl. Fl. Ned. Ind. 3: 333, 371. 1900, in clavis.

Artocarpus superba Becc. For. Borneo, 625. 1902; Merr. Philip. Jour. Sci. 18: 51. 1921, Enum. Philip. Pl. 2: 43. 1923; Ridley, Fl. Malay Penin. 3: 356. 1924. Holotype, Sarawak, *Beccari PB 2997* (FI); isotypes (FI, K).

Evergreen trees, height to 45 m. Twigs 10–20 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1.5 mm. broad, prominent; lenticels scattered. *Stipules* 4–17 cm. long, broadly ovate-lanceolate, acute, exterior rugose, subappressed-pubescent, hairs yellow to brown. *Leaves* imparipinnate; rachis 40–80 cm. (fide Elmer in Merrill, 1929, to 150 cm.) long, base to 7 mm. in diameter, terete, finely rugose; pinnae 5–12 on each side, usually in subopposite pairs with longer and shorter pairs alternating and the latter raised above the rachis, terminal pinna often bifid; juvenile leaves with distal pinnae decurrent on rachis and the pinnae pinnatifid; pinnae 3.5–40 × 2–13 cm., oblong to oblong- or ovate-lanceolate, with an acumen to 2 cm. long, the base rounded, varying cuneate, often inequilateral, glabrous, the margin entire or shallowly and distantly crenate; main veins prominent beneath, intercostals slightly so;

lateral veins 7–20 pairs, straight; intercostals parallel only towards margin; dark green, drying red-brown to pale greenish or yellowish brown; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; gland-hairs immersed, heads globose, 4–6-celled; petiolules to 40 mm. long.

Inflorescences, male and female heads usually paired in the same leaf-axil. *At anthesis: male head* 30–75 × 15–20 mm., ellipsoid-oblong, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0–2.3 mm. long, filament slender, cylindrical, anther-cells subglobose, 0.2 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.6 mm. across, pubescent; peduncle 50–65 × 4 mm., surface as in the twigs; *female head* with pubescent peltate bracts being shed and simple styles exerted to c. 1 mm. *Syncarp* to 11 × 8 cm. (fide Elmer, l.c., to 20 cm. in length), subglobose, brown, drying pale brown, covered by closely set, cylindrical, rigid, shallowly fluted, obtuse, minutely punctate processes, 6–8 × 1–1.5 mm.; wall c. 6 mm. thick; fruiting perianths numerous, proximal free region orange, pulpy, “seeds” (endocarps) ellipsoid, 17 × 10 mm.; core c. 20 mm. across; peduncle 60–130 × 10 mm., surface as in the twigs.

VERNACULAR NAMES: *Bakil*, Sumatra, Borneo; *Mentawa* or *Mentaba*, Banka, Borneo; *Puan* or *Pupuan*, Borneo.

DISTRIBUTION: in evergreen forest to 4000 ft., Malaya, Sumatra, Banka, Billiton, Lingga, Borneo.

Malaya. MALACCA: *Maingay 1483* (K, ♂, ♀). SINGAPORE: Garden Jungle, *Ridley 4113* (CAL, SING, ♂), *6429* (BM, CAL, K, SING, ♀), *6678* (BM, CAL, K, SING, ♂, ♀); MacRitchie Reservoir, s. side, *Sinclair SFN 40658* (K, ♀); Seleter Reservoir, s. side, *Sinclair SFN 39249* (L, SING). (Fide Corner, 1940, frequent in low-land forest.)

Sumatra. INDRAGIRI: Kwala Belilas, *bb 27580* (A, BO, L); Muara Serangge, *bb 29991* (A, BO, L). BENKULEN: Lebong, Bosch Pengadang, *Olivier 29* (BO, L). PALEMBANG: Banjuasin, Bajunglintjir, *NIFS E 1028* (BO, ♀), *1163* (BO, L, U, ♀); Batu-radja, *Teysmann HB 3698* (BO, K, L, U); Lematang Ilir, Gunong Megang, *NIFS E 952* (BO, K, L, SING, U, ♀), *959* (BO, L, P, U, ♂, ♀), *1029* (BO, U, ♀); Lematang Ilir, Semangus, *bb 31984* (A, BO, SING), *32042* (BO, K); Lematang Ulu, *Grashoff 277* (BO); Muara Dua, *Grashoff 454* (BO, L); Rawas, *Grashoff 1052* (BO, L). LAMPONGS: Semangka, Kuta-Agung, *Gusdorf 289* (BO, L). BANKA: Lobok Besar, *Kostermans & Anta 1230* (A, L); Muntok, Batu-balai, *Teysmann 7245* (BO, C, K, L); Sungei Liat, *Teysmann 7247* (BO, C, K, L). BILLITON: *Rossum 48* (BO, L, ♂, ♀), *Teysmann s.n.*, (BO); Tandjungpandang, *Teysmann s.n.* (BO); Tandjungpandang, Bantan, *bb 8677*, (BO, L). LINGGA: *Teysmann 7282* (BO, L, P).

Borneo. SARAWAK. *Beccari PB 2997* (FI, K, ♀); Lundu, *Foxworthy 344* (L). WEST BORNEO. *De Vriese s.n.*, 1857–61 (BO [labelled *Riedel s.n.*, Menado, Celebes], L); Sanggau, Nek Sawah, *bb 14307* (BO). SOUTH AND SOUTHEAST BORNEO. Pleihari. Kintap, *bb 8145* (BO, L); Puruktjahu, Muara Djaan, *bb 10506* (BO, L); Tanah Bumbu, Kampong Baru, *bb 13053* (BO, L, ♂). EAST AND NORTHEAST BORNEO. Balikpapan: S. Tunan, *bb 25588* (BO, L). Berouw: Domaring, *bb 18861* (BO). Bulungan: Salim Botu, S. Kumoh, *bb 11275* (BO, L). E. Kutei: Bengalon

Rapak, *bb* 15285, 15319 (BO, L); Peridan, *bb* 9862 (BO, L); Sangkulirang, Palawan, *bb* 11859 (BO, L); Sangkulirang, Ronggang, *bb* 7971 (BO, L); T. Leban, *bb* 14685 (BO, L). W. Kutei: Blu-u, *Jaheri* 1460 (BO); Ibo Antjalong, *bb* 16484 (BO, P); Kahala, *bb* 28365 (BO); Kelumpang, *bb* 16928 (A, BO, L); Longbleh, *bb* 16137 (A, BO, L), 16141 (BO), 16149 (BO, SING), 16152 (BO, P), 16488 (BO, SING); Mujup, *bb* 16752 (A, BO, L). BRITISH NORTH BORNEO. Elphinstone Prov., Tawao, *Elmer* 21600 (A, BM, BO, C, GH, K, L, P, SING, U, ♀); Kinabatangan Besar, Kori Timber Camp, *Cuadra A* 2133 (K, SING); Mt. Kinabalu, Penibukan ridge, *Clemens* 40424a, 50210 (BM); Sepilok For. Res., 15 miles w. of Sandakan, *Wood SAN* 16549 (A, K, L, ♂, ♀).

This species is the only one in *Artocarpus* to have pinnate adult leaves. It was noted by Corner (1940) that these are unusual both in that they do not disarticulate when falling, as do most compound leaves, and in the arrangement of the pinnae, with longer and shorter pairs alternating and the latter lying in a plane above the former (well shown in the photograph, l.c.). The only other occurrence of pinnate leaves in the genus appears to be in saplings of *A. tamaran*; the latter can readily be distinguished (apart from the indumentum of the shoot) by the continuous narrow wing of lamina on both sides of the rachis.

A sheet at Bogor identified under an unpublished name purports to have been collected by Riedel in Menado, Celebes, but this is presumably an error of labelling, since *De Vriese s.n.*, West Borneo, at Leiden, bears the same determination.

Merrill (1921, 1923) recorded this species (as *A. superba*) from Basilan (*Hutchinson FB* 3989), Mindanao (Zamboanga, *Merrill* 8280; Port Banga, *Whitford & Hutchinson FB* 9164; both sterile) and Palawan (*Cenabre et al. FB* 28009), but no duplicates of these collections have been traced.

2. *Artocarpus lanceifolius* Roxb. Fl. Ind. 3: 527. 1832, "*lanceaefolia*;" Wight, Ic. Ind. Or. 2: t. 679. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 122. 1847; King in Hook. f. Fl. Brit. Ind. 5: 543. 1888; King, Ann. Bot. Gard. Calcutta 2: 13. t. 11. 1889; Renner, Bot. Jahrb. 39: 366. 1907; Ridley, Fl. Malay Penin. 3: 354. 1924; Foxworthy, Malayan For. Rec. 3: 128. 2 plates. 1927; Burkill, Dict. 256. 1935; Corner, Wayside Trees, 656. t. 197. 1940.

Artocarpus lanceifolia Roxb. Hort. Beng. 103. 1814, nomen nudum.

ssp. *lanceifolius*

Evergreen trees, height to 35 m., with small buttresses, bark dark grey, peeling off in flakes. Twigs 6–8 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1 mm. broad, inconspicuous; lenticels scattered. *Stipules* 1.5–4.5 cm. long, ovate-lanceolate, acute, exterior rugose, shortly appressed-pubescent. *Leaves* 10–33 × 5–17 cm., elliptic, varying to ovate, obovate or oblong, rarely narrowly lanceolate-elliptic, short-acuminate, acumen rounded varying acute, base cuneate, decurrent, rarely inequilateral, thickly coriaceous, glabrous, the margin entire or shallowly and distantly crenate; juvenile leaves pinnatifid; main

veins prominent beneath, reticulum not or scarcely prominent; lateral veins 9–14 pairs, straight; intercostals parallel; deep green, drying pale or reddish brown with straw-coloured reticulum; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; glands deeply sunken in narrow pits, heads globose, 4–6-celled; petiole 10–30 mm. long.

Inflorescences solitary in leaf-axils or the male ones paired. *At anthesis*: *male head* 30–60 × 12–18 mm., ellipsoid to cylindrical, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, shortly bilobed above, puberulent; stamen 3.5 mm. long, filament slender, cylindrical, anther-cells oblong, 0.4 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.5 mm. across, sparsely ciliate; peduncle 25–70 × 2.5–5 mm., shortly appressed-pubescent; *female head* with pubescent peltate bracts mostly shed and bifid styles exerted to 0.5 mm. *Syncarp* to 8 × 7 cm. (to 12 cm. across, fide Foxworthy, 1927), subglobose, olive- or chestnut-brown, drying brown, tessellated from closely set, indurated, cylindrical, truncate, appressed-pubescent processes, c. 3.5 × 3 mm.; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region whitish, pulpy (fide Burkill, 1935), “seeds” (endocarps) ellipsoid, 20 × 10 mm.; core c. 15 mm. across; peduncle 50–100 × 8 mm., surface as in the twigs, or shortly appressed-pubescent.

VERNACULAR NAMES: *Keledang* or *Klidang* (Malay), Malaya, Riouw-Lingga Archip. USES: the timber is valuable and the pulp surrounding the seeds is eaten by jungle tribes.

DISTRIBUTION: in evergreen forest to 2000 ft., Malaya, Sumatra (West and East Coast), Banka, Riouw-Lingga Archip.

Malaya. PERAK. Larut: *King* 3452 (BM, CAL, K, ♂), 3826 (CAL, K, ♀); Gunong Boobo Range, *King* 7631 (CAL, K, P, SING, ♀). PAHANG: Kuala Lipis, *Phillips* 670 (SING); Temerloh, *Hamid CF* 5737 (SING). NEGRI SEMBILAN: Gunong Angsi For. Res., *Sow* 23728 (SING). MALACCA: *Maingay* 1478 (CAL, K, ♂, ♀); Bukit Sedanan Reserve, *CF* 2100 (SING, ♂); Kesang tua, *Goodenough* 1328 (BM, CAL, SING, ♀). JOHORE: Pulau Tinggi, above Kampong Tandjong Balang, *Sinclair s.n.*, May 1954 (SING); Pinerong, *Cantley* 27 (K, ♂). PENANG: Batu Ferengy, *Curtis* 3654 (CAL, K, SING, ♀); Highlands, *Curtis* 3602 (CAL, K, SING, ♂); Penang Hill, *Nanen* 35845 (SING, ♀); Puram (?) Bukit, *Curtis s.n.*, July 1893 (SING). SINGAPORE: Bukit Timah, *Corner s.n.*, Feb. 1931 (SING, ♀); Bukit Timah For. Res., Jalan Tiup Tiup, *Sinclair SFN* 40249 (K, L); Gardens Jungle, *Ridley* 6541 (BM, CAL, K, SING, ♂). (Fide Foxworthy, 1927, also in Kedah, Kelantan and Trengganu.)

Sumatra. WEST COAST: *de Vriese & Teysmann* 20 (L); Padang, Lubuk peraku, *bb* 6117 (BO); Painan, Barung Belantae, *NIFS SWK/I-50* (BO); near Pajakumbuh, Mt. Sago, *Meijer* 4708 (CGE, ♀). EAST COAST: Simelungun, Masikat, *bb* 5349 (BO, L); Sibolangit, *Lörzing* 5445, (BO, L, ♀). BANKA: *Teysmann* 7248 (BO, C, K, L, P); Muntok, Aer Limau, *bb* 7613 (BO); Sungei-elan, *Teysmann* 7250 (BO, C, K, L, P, ♀); Sungei-elan, Kampong permis, *Teysmann* 7251 (BO, P, ♀). RIOUW ARCHIP.: Bintang, *Teysmann* 7283 (BO, CAL, K, L, P, ♀). LINGGA ARCHIP. P. Sinkep: Bakong, *bb* 2045, 13670, *Kassim* 6 (BO, L); Bakong,

Santel, *bb* 17400 (BO, SING); Djago, *bb* 3945 (BO); Mapur, Marok Tuwa, *bb* 3846 (BO); Tadjur Tandjong, *bb* 8386 (BO); Tandjung Batang, *bb* 4014 (BO, L).

Roxburgh's original description was very brief and no type specimen has been found, so that the identification must rest on his drawing of a leaf and a syncarp which was published by Wight in 1843 and can be recognized with certainty as representing this species.

ssp. *clementis* (Merrill) Jarrett, stat. nov.

Artocarpus clementis Merr. Jour. Str. Br. Asiat. Soc. 85: 164. 1922. Holotype, British North Borneo, *Clemens* 10770 (PNH, not seen, photograph in A); isotypes (A, BO, K).

Differs from ssp. *lanceifolius* as follows: *leaves* varying to ovate-elliptic or ovate-lanceolate; *syncarp* covered by somewhat widely spaced, indurated, slightly tapering, obtuse, appressed-pubescent processes, 1–1.5 × 1 mm., with scattered peltate bracts persistent between them; wall c. 3 mm. thick; "seeds" (endocarps) numerous, ellipsoid, 12–15 × 8 mm.; core c. 15 mm. across; peduncle 40 × 6 mm., minutely punctate.

VERNACULAR NAME: *Keledang* (Malay).

DISTRIBUTION: in evergreen forests to 3600 ft., endemic to northeastern Borneo.

Borneo. EAST AND NORTHEAST BORNEO. Balikpapan: Pemaaluan, *bb* 24763 (BO, L); S. Karnain, *bb* 26374 (BO, L, SING). Berouw: Betemaran Tidi, *bb* 19062 (BO); Domaring, *bb* 18831 (A, BO), *bb* 18835 (A, BO, L), 18851 (BO); Inaran, *bb* 12078 (BO); Long Lanuk, *bb* 18445 (BO), 18461 (BO, L, SING). Bulungan: Kabiran, S. Bengalun, *bb* 11686 (BO); Mara, *bb* 10750 (BO). E. Kutei: Muara Karangan, Remendai, *bb* 7962 (BO); Sangkulirang, Palawan, *bb* 11867 (BO); Sangkulirang, Pingadan, *bb* 12992 (BO); Sangkulirang, Rantau Banan, *bb* 15236, 15238, 15247 (BO); Loa Djanan, w. of Samarinda, *Kostermans* 6627 (K, L, ♂); Tandjong Bangko, nr. Mahakam River estuary, *Kostermans* 7096 (BO, K, L, ♀). W. Kutei: Djembajan, Sungei Djambu, *bb* 24672 (A, BO, L); Kendisi, *bb* 16681 (BO, L), 16695 (A, BO, L); Mo-Antjalong, *bb* 16482, 16486 (A, BO, L); near Mt. Kemul, *Endert* 3683 (L). Tidung: Loban, *bb* 17882 (BO, L). BRITISH NORTH BORNEO. Mt. Kinabalu, *Foster & Puasa* 3522 (K); Mt. Kinabalu, Gurulau Spur, *Clemens* 10770, Nov. 1915 (A, BO, K, ♀); 12 miles w. of Ranau, Bondu Tahan, *Wood & Charrington SAN* 16381 (A, ♀). NUNUKAN, *bb* 26174 (BO).

The description of the syncarp is based on that of the type of *Artocarpus clementis*, which is slightly decayed, but almost certainly had the processes rather widely spaced at maturity. In the other, younger, syncarps seen from Borneo the processes are also small but they are closely set and apparently separate only when the syncarp nears maturity. The three collections cited from British North Borneo have rather distinctive ovate-elliptic to ovate-lanceolate leaves, but they merely represent an extreme of the range of variation which is exhibited by the rest of the material seen from Borneo, nearly all sterile, and which is not separable from that of the species as a whole. In view of the discontinuity in the distribution of the species between a western area including Malaya and Sumatra and a smaller area

to the east in northeastern Borneo, it is likely that only ssp. *clementis* is represented in the latter. The sterile collections from Borneo are tentatively listed under this subspecies, but only specimens bearing syncarps or showing the extreme leaf-shape can be assigned here with certainty.

Series **Asperifolii** Jarrett, ser. nov.

Ramuli et folia hispida vel hispida-pubescentes; folia sine hypoderme, glandulis subimmersis, capitibus globosis, 4–16-cellis; inflorescentiae masculae globosae ad clavatae.

TYPE SPECIES: *Artocarpus rigidus* Blume.

3. **Artocarpus melinoxylus** Gagnep. Bull. Soc. Bot. Fr. 73: 87. 1926, "*melinoxyla*;" Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 736. 1928. Syntypes, Indochina, *Chevalier* 37007, *Poilane* 1218, 4588, 6873, 7079, 7621 (P); lectotype *Poilane* 7079 (P).

ssp. **melinoxylus**

Trees, height to 15 m. *Twigs* 3–7 mm. thick, rugose, hispid, hairs yellow, appressed (longer and patent on juvenile shoots); annulate stipular scars 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* c. 2.5 cm. long, ovate, acute, hispid-pubescent, hairs yellow, subappressed. *Leaves* 7–30 × 4–18 cm. (–35 × 25 cm.) elliptic to obovate- or ovate-elliptic, short-acuminate, base rounded, varying cuneate, margin entire; main veins only prominent beneath or intercostals slightly so; glabrous above or with scattered hairs on the main veins, appressed subhispid-pubescent on the main veins beneath; lateral veins 6–13 pairs, straight, intercostals parallel; drying pale to dark red-brown, lighter beneath; hypodermis absent; glands half immersed, heads globose, 6–8-celled; petiole 8–28 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* (one only seen at maturity) 50 × 45 mm., subglobose, smooth, covered by flowers and bracts; perianths deeply 2 (or 3)-lobed, 1 mm. long; stamen 1.5 mm. long, filament slender, cylindrical, anther-cells ellipsoid, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.4 mm. across, these and perianths sparsely ciliate; peduncle 50 × 3 mm., appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exerted to 1.0 mm. *Syncarp* to 6 cm. across, globose, drying red-brown, covered by closely set, indurated, cylindrical, obtuse, hispid processes, c. 3 × 2 mm., hairs patent and slightly crisped; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region fleshy, "seeds" (pericarps) ellipsoid, 10 × 6 mm.; core 20–25 mm. across; peduncle 70–135 × 6 mm., appressed-hispid.

VERNACULAR NAME: *Cay mit nai*, Annam. USES: the wood is stated in field notes to be of good quality.

DISTRIBUTION: in forests to 5000 ft., endemic to Indochina.

Indochina. ANNAM. Near Huê, Nui Bah Ma, *Poilane* 29977 (p, ♀). Near Nhatrang: Massif de Cô Ihn, *Poilane* 4588, Sept. 1922 (p, ♀); Massif de la Mère et l'Enfant, *Poilane* 6873, May 1923 (p, ♀). Quang Tri prov., Mai Lanh, *Poilane* 1218, Mar. 1920 (κ, p, ♂). Near Tourane: *Clemens* 3431 (p, ♂); Balet, *Clemens* 4021 (κ, p, ♀); Ba na, *Poilane* 7079, Aug. 1923 (A, p, ♀); Mt. Bani [Ba na], *Clemens* 3510 (A, κ, p, ♀); Lien Chien, *Poilane* 7621, Aug. 1923 (A, p, ♀); Thua-Luu div., Lang-co For. Res., *Chevalier* 37007, Apr. 1918 (p, ♂). LAOS. Luang Prabang prov., n.e. of M. Ngai [probably Muong Ngoi], *Poilane* 20689 (p, ♂).

ssp. **brevipedunculatus** Jarrett, ssp. nov. Holotype, British North Borneo, *Wood SAN A 1733* (A); isotype (κ).

Differt ab typo *inflorescentiis ad anthesin capitulis masculis subglobosis*, c. 15 mm. diametro, pedunculis, 8–17 × 2.5 mm. suffultis, *femineis* pedunculis 13–18 × 3 mm. suffultis [in syncarpio submaturo ad 25 mm. longis].

VERNACULAR NAME: *Temponek*.

DISTRIBUTION: in lowland forest, endemic to British North Borneo.

Borneo. BRITISH NORTH BORNEO: Beaufort, *Wood SAN A 1733*, May 1955 (A, κ, ♂, ♀); Jesselton, *Daw Kepong FN 71664* (A, κ, ♀).

This new subspecies agrees closely with the type from Indochina, except in the smaller size of the male head and in the length of the peduncles. The elongation of the latter, throughout the genus, occurs largely before anthesis and they can be assumed to be considerably shorter than in ssp. *melinoxylus*, even in the mature syncarp. In spite of the difference in the size of the male inflorescence in the two subspecies the dimensions of the flowers are the same; the perianths are unusual for this subgenus in that they are very deeply lobed.

Although taxonomically *Artocarpus melinoxylus* is very near *A. chaplasha*, it differs in a number of characters which appear to justify maintaining it as a distinct species. The male inflorescence in *A. chaplasha* has a longer, more slender peduncle and the flowers are larger in all their parts, while the perianth is only shortly bilobed. The indumentum of the syncarps is also different, being appressed on the syncarp processes in *A. chaplasha* instead of patent and slightly crisped. In *A. chaplasha* the leaves have the entire upper surface and the venation beneath subappressed hispid-pubescent, but in *A. melinoxylus* the leaves have a smooth upper surface and only the main veins are appressed hispid-pubescent beneath.

4. **Artocarpus chaplasha** Roxb. Hort. Beng. 66. 1814, nomen nudum, Fl. Ind. 3: 525. 1832; Wight, Ic. Ind. Or. 2: t. 682. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 112. 1847; Kurz, For. Fl. Burma 2: 432. 1877; King in Hook. f. Fl. Brit. Ind. 5: 543. 1888; King, Ann. Bot. Gard. Calcutta 2: 13. t. 12. 1889; Renner, Bot. Jahrb. 39: 365. 1907; Troup, Silvicult. Ind. Trees 3: 880. t. 325. 1921; Parkinson, For. Fl. Andaman Is. 254. 1923; Champion, Indian For. 60: 524. t. 50. 1934. Holotype, "East India," *Roxburgh s.n.* (κ).

Artocarpus chama Buch.-Ham. ex Wall. Cat. no. 4657C. 1831, nomen nudum.

Urostigma chrysophthalmum Miq. Hook. Lond. Jour. Bot. 6: 575. 1847.

Ficus chrysophthalma Miq. Ann. Mus. Lugd.-Bat. 3: 285. 1867.

Deciduous trees, height to 40 m., bark grey, becoming brown, peeling off in flakes. *Twigs* 4–10 mm. thick, rugose, densely hispid-pubescent, hairs yellow, appressed (patent on juvenile shoots); annulate stipular scars c. 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* 1.5–2.5 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow, appressed. *Leaves* 14–23 × 9–14 cm., obovate-oblong, varying obovate or elliptic, acute, base rounded or shallowly cordate, margin entire; juvenile leaves pinnatifid; main veins prominent beneath, intercostals slightly so; very shortly subappressed-hispid above, venation beneath shortly subappressed hispid-pubescent, both surfaces varying subglabrous; lateral veins 8–12 pairs, straight; intercostals parallel; green, drying pale or reddish brown, lighter beneath; hypodermis absent; glands half immersed, heads depressed-globose, c. 8-celled; petiole 8–30 (–40) mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 15–30 × 10–30 mm., ellipsoid to short-obovoid or subglobose, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, bilobed above, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindrical, anther-cells ellipsoid, 0.3 mm. long; bracts slenderly stalked, the heads peltate, to 0.5 mm. across, pubescent; peduncle 60–75 × 1.5 mm., shortly appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exerted to 0.5 mm. *Syncarp* to 6 cm. [to 10 cm., fide King, 1889] across, subglobose, yellow, drying brown, covered by closely set, indurated, cylindrical, obtuse, appressed-hispid processes, c. 1.5 × 2 mm.; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region . . . , “seeds” (pericarps) ellipsoid, 7 × 4 mm. [fide King, 1889, to 20 mm. long]; core c. 20 mm. across; peduncle 55–80 × 3 mm., appressed hispid-pubescent.

VERNACULAR NAMES: *Chaplash* (Bengali), India; ⁴ *Taung-peing*, Burma. USES: an important timber tree and often planted, although Champion (1934) stated that elephants found the seedlings very palatable; Parkinson (1923) noted that the leaves were used for elephant fodder and the fruits were edible.

DISTRIBUTION: in evergreen, semi-evergreen and moist deciduous forest to 5000 ft., in regions with a monsoon climate (rainfall at least 80 inches), northeastern India (Sikkim to Assam and Chittagong), Lower Burma (to northern Tenasserim), Andaman and Nicobar Is.

India. Not localized: East India, *Roxburgh s.n.* (K); Dulka Thae, *Gamble 1180A*, Jan. 1873 (K); Majoojah forests, *Brandis 331*, Jan. 1862 (BM). SIKKIM: *Anderson s.n.* (BO), *Hooker f. & Thomson s.n.* (CAL, GH, P), *Kurz s.n.* (CAL); Terai, Tin sing tung, *sine nom. et num.* (K). WEST AND EAST BENGAL: Duars,

⁴ Throughout this series of papers the word India will be used in a geographical sense, to denote the Indian subcontinent, and will include the modern political subdivisions of India and Pakistan.

Talpaigwa, *Haines 529* (κ); towards Ilafoo, *Griffith 4668* (κ); Tipperah (Hill), near Ranir Bazar. Noagaon, *Debbarman 1096* (CAL, ♀). ASSAM: *Lister s.n.* (CAL), *Mann s.n.* (CAL, ♂), *Masters s.n.* (BO, L, P); Abor, Pilung, *Burkill 38127* (CAL); Gowhatly, *Clarke 37165A* (BM); [? =] Guwalatty, near Aber [? Abor], *Jenkins s.n.*, Apr. 1835 (CAL); Cachar, Bundookmora, *Keenan s.n.* (κ); Jatookia, *Watt 11308* (BM, ♂); Kamrup, *sine nom. 942* (CAL, ♂); Khasia Hills, *Hooker f. & Thomson s.n.* (A, BM, C, L, P, U); Khasia Hills, Doodputli, *Hooker f. & Thomson s.n.*, Nov. 1856 (κ); Mangeldai to foot of Bhutan Himalaya, *Schlagintweit 13480* (BM); Naga Hills, *Mohassi 214* (L); Nowgong, *Hooker f. & Thomson s.n.*, July 1850 (κ); Sibsagar, Ligri Pukri, *Watt 10405* (CAL, ♀). CHITTAGONG: Kagi Ke Hath, *Hooker f. & Thomson s.n.*, Jan. 1851 (κ); Kodala, *Hooper 26008* (CAL), *King 392, 487* (BM, CAL, ♀); Rangamati, *Lister s.n.* (CAL); Rangamati, Magban, *Hooper s.n.*, Nov. 1898 (CAL); Rangamati and Damara, *Wallich 4657C* (BM); Seetakoone, *Hooker f. & Thomson s.n.*, Jan. 1851 (κ).



FIG. 11. Distribution of the species of sect. DURICARPUS. 1, *Artocarpus anisophyllus* (? also in the Philippines); 2, *A. lanceifolius*, a, ssp. *lanceifolius*, b, ssp. *clementis*; 3, *A. melinoxylus*, a, ssp. *melinoxylus*, b, ssp. *brevipedunculatus*; 4, *A. chaplasha*; 5, *A. odoratissimus* (probably introduced in the areas enclosed by broken lines); 6, *A. hispidus*; 7, *A. rigidus*, a, ssp. *rigidus*, b, ssp. *asperulus*.

Lower Burma. (?) *Abel s.n.* ["East Indies"] (*K*, ♂); Pegu, Tonkyeghat, *Kurz 1498* (CAL p.p., *L*, ♀), *1499* (CAL); Rangoon, *Dickason 5528, 6948* (A), *McClelland s.n.* (*K*, ♂). **TENASSERIM.** Kyauktalon [not located], *Meebold 14612* (CAL, ♂). Thaton: Martaban, *Kurz 1498* (CAL p.p., ♀). **Andaman Islands.** *Kurz s.n.*, Nov. 1881 (CAL), *Parkinson 167* (DD, ♂), *Rogers s.n.*, 1904 (*K*, ♂, ♀); Manglutan, *Parkinson 463* (*K*, ♂ ♀); South Andaman, *King s.n.*, Apr. 1890 (CAL), *Kurz s.n.* (*K*, ♀); South Andaman, n. coast, *Kurz s.n.* (*K*, ♀); S. Andaman, S. Corbyn's Cove, *Kurz s.n.* (CAL). **Nicobar Islands.** *Jelinek 165* (CAL, ♂); Karnicobar, Kakena, *Kamphovener 2672* (C); Karnicobar and Chowry, *Kamphovener 2394* (C); Teressa, *Kamphovener 2741, 2742* (C).

Cultivated. INDIA: Calcutta, Hort. Bot., *Lane 7935* (CAL, ♂), *Wallich 4657* (*K*, ♂), *4657D* (BM, CGE, P, ♂), *s.n.*, Apr. 1815 (C); Dehra Dun, Forest Research Institute, *Raizada s.n.*, May 1947 (DD, ♂, ♀), *s.n.*, June 1950 (DD, ♀).

Artocarpus chaplasha is somewhat similar vegetatively to *A. rigidus* ssp. *asperulus* (in addition to *A. melinoxylus*, the distinguishing characters of which have been given above), but it may be identified by the larger, typically obovate-oblong leaf, since in Tenasserim where the two entities may overlap, the leaf shape of *A. rigidus* ssp. *asperulus* tends to ovate. It is, however, of interest to note that the distributional areas of these three entities, and hence, presumably, their ecological requirements are complementary. *A. chaplasha* is restricted to areas with a moderate to well-marked monsoon climate (but a rainfall of at least 80 inches) and is recorded definitely as far south as the Thaton district of Tenasserim. *A. rigidus* ssp. *asperulus* is recorded only as far north as the adjacent Amherst district (there is one unlocalized collection by Meebold of each species) and occurs, primarily in coastal areas, in the moister peninsular regions of Burma and Siam, extending to Cambodia and southern Annam; it is replaced by *A. melinoxylus* in the mountains of Annam and northeastern Laos, which have a rather more uniform, though not more abundant, rainfall.

5. *Artocarpus odoratissimus* Blanco, Fl. Filip. 671. 1837, "*Arctocarpus odoratissima*;" Fern.-Villar, Noviss. App. 203. 1880; Elmer, Leaflet. Philip. Bot. 2. 618. 1909; Wester, Philip. Agr. Rev. 8: 108. *t. 7d, 9b*. 1915. 17: 24. 1924(a), Bull. Bur. Agr. Philip. 39: 129, *t. 15b, 32b*. 1924(b); Merr. Jour. Str. Br. Asiat. Soc. 76: 80. 1917, Sp. Blancoanae. 124. 1918, Enum. Philip. Pl. 2: 42. 1923. Neotype, Mindoro, *Merrill SB 1019* (BM).

Artocarpus tarap Becc. For. Borneo, 626. 1902; Renner, Bot. Jahrb. 39: 365. 1907. Syntypes, Sarawak, *Beccari PB 9, PB 2528, PB 2588, PB 2697* (FI); lectotype, *Beccari PB 2697* (FI).

Artocarpus mutabilis Becc. For. Borneo, 627. 1902; Renner, Bot. Jahrb. 29: 365. 1907. Holotype, Sarawak, *Beccari PB 758* (FI); isotypes (FI, *K*, P).

Evergreen trees, height to 25 m. Twigs 4–10 mm. thick, rugose, hispid-pubescent, hairs yellow to rufous, patent; annulate stipular scars c. 0.5 mm. wide, not raised; lenticels scattered. *Stipules* 1–8 cm. long, ovate, acute, hispid-pubescent, hairs yellow to rufous, appressed or patent. *Leaves* 16–50 × 11–28 cm., broadly elliptic to obovate, obtuse to shortly acumi-

nate, base cuneate, often slightly decurrent, margin entire or distantly and shallowly crenate, often bearing tufts of hairs towards and at apex, varying lobed in upper half, lobes one (rarely two) on each side; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; both surfaces subappressed hispid-pubescent, scabrescent above, with the main veins softly and densely yellowish pubescent; lateral veins 13–15 pairs, straight; intercostals parallel; dark green, drying reddish to blueish brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose (8–)16-celled, cells in two tiers; petiole, 20–30 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 40–90 × 25–35 mm., ellipsoid to clavate, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0 mm. long, filament slender, cylindric, anther-cells subglobose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, pubescent; peduncle 25–70 × 3–5 mm., indumentum as shoot; *female head* with pubescent peltate bracts mostly shed and simple styles exerted to c. 1.5 mm. *Syncarp* to 16 × 13 cm., subglobose, greenish yellow, drying pale red-brown, covered by closely set, rigid, cylindric, hispid processes, 8–13 × 1 mm., fluted below, the tips clavate; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region white, juicy (fide Wester, 1915), “seeds” (pericarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 55–140 × 8 mm., indumentum as shoot.

VERNACULAR NAMES: *Oloi* or *Loloi*, Mindoro; *Marang* or *Madang*, Mindanao, Basilan, Sulu; *Terap* (Malay), Borneo. USES: the syncarp is esteemed, particularly in the Philippines, for the sweet, juicy, aromatic perianths surrounding the seeds, which may also be roasted; according to Wester (1915) the flavour is better than that of the Jack.

DISTRIBUTION: in evergreen forest to 3000 ft., Borneo; in regions with abundant and equally distributed rainfall (? introduced), Philippines (Mindoro, Mindanao, Basilan, Sulu Archip.).

Borneo. *Korthals s.n.* (L, U). SARAWAK. *Haviland 3116C* (CAL, ♂, ♀); Upper Rejang River, Gat, *Clemens s.n.*, July 1922 (NY); Gunong Mattan, *Beccari PB 2528*, Nov. 1866 (FI, K), *2588*, Nov. 1866 (FI, K, P, ♂, ♀); Kuching, *Beccari PB 2697*, Nov. 1866 (FI, K, ♀), *Haviland 2190* (CAL, K, SING, ♂, ♀), *Haviland & Hose 3316* (K, ♂, ♀), *3316B* (BM, L, ♂, ♀); base of Santubong, *Sinclair SFN 38372* (K, SING, ♀); Siul, nr. Kuching, *Beccari PB 758*, Oct. 1865 (FI, K, P, ♂, ♀). WEST BORNEO. *De Vriese s.n.* (K); Landak, *s. nom. et num.* (BO); Liang gagang, *Hallier 2577* (BO); Melawie, Tjatil B. Tengkujung, *bb 26328* (BO, L). SOUTH AND SOUTHEAST BORNEO. Muara Teweh, Lué Katjang, *bb 10926* (BO); Puruktjahu, Muara Djaan, *bb 10514* (BO). EAST AND NORTHEAST BORNEO. Berouw: Dedemuaer, *bb 19103* (A, BO, L); Tandjong-redeb, Labanan, *bb 11520* (BO). Tidung: *bb 17732* (BO); G. Muara Tagel, *Amdjah 136* (BO, L, ♀). W. Kutei: Blu-u, *Jaheri 1488* (BO). BRITISH NORTH BORNEO. *Burbridge s.n.*, 1877–78 (BM, K); Kabili-Sepilok For. Res., *Puasa Herb. For. Dept. B.N.B. 7037* (SING); Mt. Kinabalu, Dallas, *Clemens 26228* (A, BM, BO, L, NY, SING, ♀); Tenom, Pangie mile 80, *Cuadra A 3282* (L, SING). SIBATIK. St. Lucia, *Cuadra*

A 2403 (K, L). NUNUKAN. *bb* 26196 (BO, L). TARAKAN. N. E. Kalimantan, Passangrahan, *Meijer* 1851 (K, L, ♀).

Philippine Islands. MINDORO. Calapan, *Merrill* 2583 (US, ♂), *SB* 1019, May 1916 (A, BM, BO, GH, K, L, P, ♀); Pinamalayan, *Ramos* *BS* 41090 (A, ♀); Upper Sinariri River ("near house"), *Conklin* *PNH* 17522 (A, L, PNH, ♀). MINDANAO. Davao: *Wester* *BS* 19356 (K, ♀). Lanao: near Abaga ("probably planted"), *Lynn Zwickey* 243 (A, ♂). Zamboanga: *Ramos & Edano* *BS* 37469 (A, BM, L, ♀). BASILAN. *Hallier* 4504 (L), *Merrill* *SB* 1018 (A, BM, BO, GH, K, L, P), *Miranda* *FB* 17880 (K, P, ♂), *Reillo* *FB* 15416 (L), *Wester* *BS* 38345 (A); San Rafael, Moro, *Hutchinson* *s.n.*, May 1906 (NY). SULU ARCHIP. Jolo, *Vidal* 3846 (K). **Cultivated.** BORNEO. Sarawak, *Beccari* *PB* 9, May 1865 (FI, K, P, ♂); Sandakan, *Villamil* *Herb. For. Dept.* *B.N.B.* 200 (L). MAURITIUS. *Chapelier* *s.n.*, *Commerson* *s.n.* (P).

Apart from the very characteristic inflorescences, this species can be recognized by the length of the indumentum on both surfaces of the leaves. In *Artocarpus elasticus*, which may be confused with *A. odoratissimus* when sterile, the leaves are also markedly scabrid above, but from very short appressed hairs.

Although this species was described from and is better known in the Philippines, its distribution there is limited and it was probably introduced to the islands from Borneo, where it was described under the names *A. mutabilis* and *A. tarap* by Beccari. The second of these was reduced to *A. odoratissimus* by Merrill (1917) and later he stated (1924) that the species apparently was always planted in the Philippines, which is confirmed by such field notes as are available (quoted above). Wester (1924a) also noted a tradition of the Moros in the southwestern Philippines that the Marang was introduced by them from the west.

6. *Artocarpus hispidus* Jarrett, sp. nov. Holotype, Singapore, *Corner* *SFN* 37035 (SING); isotype (K).

Differt ab *A. rigido* capitulis masculis longiore pedunculatis, ramulis juvenilibus pedunculisque dense hispidi-pubescentibus, pilis patentibus.

Arbores [ad 20 m. altae]. *Ramuli juniores* 4–7 mm. crassi, plus minusve rugosi, dense hispidi-pubescentes, pilis rufis patentibus; cicatrices stipularum annulatae, 0.5 mm. latae, non prominentes, nec conspicuae; lenticellae rarae. *Stipulae* 0.5–1 [–2] cm. longae, ovatae, acutae, dense subappresseque hispidae, pilis rufis. *Folia* 15–19 × 7–8 [12–23 × 5–10] cm., obovati-elliptica [vel elliptica], acuta [vel breviter acuminata] basi cuneata, margine versus apicem denticulata [vel integra], supra scabrida, pilis brevissimis appressis prae fractisve, basibus inflatis tuberculatis, costa nervis lateralibusque dense appresseque pubescentibus, subtus hispidi-pubescentia, saturata virida, in sicco rubri-brunnea, vel supra canescentia; folia juvenilia pinnatifida; costa nervi lateralesque subtus prominentes; nervi transversales venulaeque subtus prominuli; nervi laterales utrinque [11–]14–15, recti; nervi transversales paralleli; hypodermis absens; glandulae subimmersae, capitibus globosis, 4–8-cellis; petiolus 10–15 [–20] mm. longus.

Inflorescentiae axillis foliorum solitariae [vel geminae]. *Ad anthesin*: *capitula mascula* [15–]30 × [15–]20 mm., obovoidea, plana, floribus bracteisque numerosissimis obtecta; perianthia tubulosa, 0.6 mm. longa, supra bilobata, minute pubescentia; stamina 0.7 mm. longa, filamentis tenuis, cylindricis, cellis antherum globosis, 0.1 mm. longis; bractee tenuiter stipitatae, capitibus peltatis, ad 0.3 mm. latis, pubescentibus; pedunculus 25[12–30] × 2 mm., indumento ut ramulis; *capitula feminea* bracteis peltatis pubescentibus subdeciduis, stylis simplicibus 1.5 mm. longis exsertis. *Syncarpia* ad 5.5 cm. diametro, globosa, in sicco fulvi-brunnea, echinata, processibus crebris, rigidis, teretibus, obtusis, hispidis, 5–6 × 1 mm.; stratum externum syncarpium c. 2 mm. crassum; "semina" (pericarpia indurata) numerosa, ellipsoidea, 13 × 10 mm., perianthiis liberis carnosisque inclusa; axis syncarpium c. 15 mm. diametro; pedunculus 25–35 × 5 mm., indumento ut ramulis. (Inflorescentiae typi spiritu vini conservae descriptae.)

DISTRIBUTION: in evergreen forest to 1000 ft., endemic to Malaya.

Malaya. PERAK: Goping, *Scortechini* 1979 (BM, CAL, K, SING, ♂, ♀). TRENGGANU: Kg. Binjai, on road to K. Brang, *Corner s.n.*, Apr. 1937 (SING). SELANGOR: Sungei Buloh For. Res., *Ja'amat & Jackson SFN 39416* (A. L. ♂). MALACCA: *Cantley s.n.* (SING, ♂). PENANG: Government Hill, *Curtis s.n.*, Mar. 1894 (SING). SINGAPORE: Bukit Timah, *Corner SFN 37035*, June 1940 (K, SING, ♂, ♀). *Corner s.n.*, Mar. 1941 (SING, ♂); Changi, *Ridley 3357* (BM, CAL, SING, ♀); 11½ miles Mandai road, *Sinclair SFN 40051* (L); Reservoir jungle, Thompson Reach end, *Corner s.n.*, Jan. 1937 (SING); Sangli, *Ridley 6756* (SING, ♂). Cultivated. SINGAPORE: Hort. Bot., *Ahmad s.n.*, Mar. 1926 (SING, ♂).

The syncarps of *Artocarpus hispidus* and *A. rigidus* are very similar but the two species are quite distinct in the length of the male peduncles and the indumentum of the shoot and peduncles, and the differences were noted by Corner on the type. *Artocarpus hispidus* also differs from *A. rigidus* ssp. *rigidus* in the scabrid upper surface of the leaf, and from ssp. *asperulus* in the leaf shape. King's description of *A. rigidus*, under which he cited *Scortechini* 1979, also included this species.

7. *Artocarpus rigidus* Blume, *Bijdr.* 482. 1825, "*rigida*;" *Tréc. Ann. Sci. Nat. Bot.* III. 8: 114. 1847; Miq. in *Zoll. Syst. Verz. Ind. Archip.* 2: 89, 95. 1854; Miq. *Fl. Ind. Bat.* 1(2): 286. 1859, *Suppl.* 418. 1861. *Ann. Mus. Lugd.-Bat.* 3: 211. 1867. *Kurz, For. Fl. Burma* 2: 431. 1877; King in *Hook. f. Fl. Brit. Ind.* 5: 540. 1888; King, *Ann. Bot. Gard. Calcutta* 2: 8. *t.* 3. 1889; *Koord. & Val. Bijdr. Boomsoort. Java* 11: 17. 1906; Renner, *Bot. Jahrb.* 39: 366. 1907; Ridley, *Fl. Malay Penin.* 3: 352. 1924; Corner, *Wayside Trees*, 657. *t.* 198, 199. 1940; Backer, *Beknopte Fl. Java* 6: 14. 1948. Holotype, Java, *Blume 1364* (L); isotype (CAL).

Artocarpus runcinata Reinw. ex Blume, *Cat. Bog.* 101. 1823, nomen nudum. *Artocarpus echinata* Roxb. *Hort. Beng.* 66. 1814, nomen nudum. *Fl. Ind.* 3:

527. 1832; Wight, Ic. Ind. Or. 2: t. 680. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 113. 1847. Holotype, *Roxburgh s.n.* (BM).
- Artocarpus cuspidatus* Griffith, Not. Pl. Asiat. 4: 400. 1854. Holotype, Malacca, *Griffith 4664* (κ).
- Artocarpus kertau* Zoll. ex Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854; Miq. Fl. Ind. Bat. 1(2): 287. 1859; Koord. Exkursionsfl. Java 2: 95. 1912. Holotype, Java, *Zollinger 1009* (P); isotypes (L, U).
- Artocarpus dimorphophylla* Miq. Fl. Ind. Bat. Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teysmann HB 3369* (U); isotype (BO).
- Artocarpus varians* Miq. ll.cc. Holotype, Sumatra, *Teysmann HB 4358* (U); isotypes (BO, L).
- Artocarpus muricata* Hunter ex Ridley, Jour. Str. Br. Asiat. Soc. 53: 114. 1909, pro syn.

ssp. **rigidus**

Evergreen trees, height to 35 m., buttressed, bark grey, peeling off in flakes. *Twigs* 2–6 mm. thick, smooth or rugose, densely to sparsely hispid, hairs rufous, appressed; annulate stipular scars c. 0.5 mm. broad, inconspicuous; lenticels few, scattered, or none. *Stipules* 0.5–3 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow or rufous, appressed. *Leaves* 9–32 × 5–15 cm., elliptic to ovate-, obovate- or oblong-elliptic, apex acute or short-acuminate, varying obtuse, base cuneate, varying narrowly rounded, margin entire or distantly and shallowly crenate; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; glabrous and smooth above, or rarely slightly scabrid from sparse, very short, appressed hairs, except the appressed-pubescent main veins, venation appressed-hispid beneath; lateral veins (9–)12–20 pairs, straight; intercostals parallel; dark green, drying blue-grey to red-brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose, 8-celled, cells in two tiers; petiole 10–25 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 13–20 mm. across, short-obovoid to globose, smooth, covered by flowers and bracts; perianths tubular, 1.2 mm. long, shortly bilobed above, minutely pubescent; stamen 1.3 mm. long, filament slender, cylindrical, anther-cells globose, 0.1 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, shortly ciliate; peduncle 2–6 × 2.5 mm., densely appressed hispid; *female head* with pubescent peltate bracts being shed, and simple styles exerted to c. 5 mm. *Syncarp* to 7 cm. across (to 13 cm. fide Corner, 1940) globose, dull orange, drying pale brown, echinate from closely set, rigid, tapering, fluted, acute, hispidulous processes, 7–9 × 1.5 mm.; wall c. 10 mm. thick; fruiting perianths numerous, proximal free region orange, fleshy, "seeds" (pericarps) ellipsoid, 12 × 7 mm.; core c. 20 mm. across; peduncle 8–25(–40) × 8 mm., appressed hispid.

VERNACULAR NAMES: *Perian*, Malaya, *Purian* or *Surian*, Sumatra, *Pujan*, Borneo (Malay); *Tempunai* or *Tempunih*, Malaya, *Tempunit*, Sumatra (Malay); *Pussar*, Java (Sundanese). USES: the tree is cultivated for its

fruit in Malaya and Java, the edible portion being the sweet, pulpy, waxy perianths surrounding the seeds; it also provides timber.

DISTRIBUTION: in evergreen forest to 1500(-3000) ft., noted several times as occurring near streams, Tenasserim, Malaya, Sumatra, Simalur, Banka, Billiton, Riouw-Lingga Archip., Borneo, Java (except the eastern province).

Lower Burma. TENASSERIM: *Helper* 4669 (CAL, K, ♂). **Malaya.** KEDAH: Bukit Rombang, *Dmat Kepong FN* 27377 (K, ♂); Cherok Perah, *Meh CF* 17779 (SING); Katumbah, *Meh CF* 17882 (SING). PERAK: *King* 6921 (CAL, K, ♂, ♀); Batang Padang district, *King* 7755 (CAL, K, L, P, ♀); Bikum Sungei, *Murdoch* 376 (BM); Larut, *King* 6727 (CAL, K, ♂); Larut, Turu, *King* 6751 (CAL, L, P, ♂); Larut, Turu, Gunong Bubu range, *King* 7612 (CAL, SING, ♀), 7679 (CAL, K, ♂, ♀); Matang Jambu, *Wray* 2528 (CAL, SING, ♀); Teluk Anson, *Allen* 37244 (A, BO, K, SING). TRENGGANU: Ulu Brang, *Moysey & Kiah* 33745 (SING). PAHANG: Gat, near Raub, *Burkill & Haniff* 16929 (SING); Kuala Lipis, *Nong CF* 1258 (SING); Temerloh, *Awang CF* 2398 (SING), *Kassim CF* 0731 (SING, ♂). SELANGOR: Bukit Badat res., Rawang, *Bahsin CF* 32403 (SING); Kuala Lumpur, *Hose CF* 4599 (K, SING, ♀); Sungei Buloh For. Res., *Hashim* 37 (K, ♂); Weld Hills Res., *Hamid CF* 4575 (K, ♀). NEGRI SEMBILAN: *Franck* 1197 (C). MALACCA: *Alvins* 590, 1070, 1234, 1317 (SING), 1624 (SING, ♀), *Maingay* 1474 (CAL, K, L, ♂, ♀), 1475 (K), 1476 (CAL, GH, K, L, ♂, ♀); Batu Tiga, *Holmberg* 766 (SING); between Roombiya and Aloor Gafah, *Griffith* 4664, Sept. 1842 (K); 14-14½ miles Sungei Udan For. Res., *Sinclair SFN* 40597 (K, SING). JOHORE: Gunong Pantai, *Corner s.n.*, Jan. 1937 (SING); Sungei Pelepah Kiri, *Corner s.n.*, June 1937 (SING). PENANG: Government Hill, *Curtis s.n.*, Mar. 1894 (SING, ♀); Penaea Bukit, *Curtis* 1984 (SING); Penang Hill, *Nanen s.n.*, June 1940 (SING); Waterfall, *King s.n.*, Aug. 1879 (CAL); Waterfall Quarry, *Curtis* 3603 (CAL, K, SING, ♀). SINGAPORE: Changi, *Ridley* 3357 (K), 4437 (CAL, SING, ♂, ♀); Garden Jungle, *Ridley* 6542 (BM, CAL, K, ♂, ♀).

Sumatra. *De Vriese* 23 (L), *De Vriese & Teysmann* 18 (L). TAPANULI: Barus, Pardamuan, *bb* 31402 (A, BO, L); Padang Lawas, Gunong Tua Djulu, *bb* 6443 (BO). WEST COAST: Ayer Waringun, *Burck s.n.*, Aug. 1883 (BO, L); Priaman, *Diepenhorst HB* 7292 (BO, P), *Teysmann* 754 (BO); Sinkara, *Teysmann HB* 756 (BO, CAL, L, U). EAST COAST: Huta Padang, Asahan, *Krukoff* 4376 (A, BO, L, SING, ♀); Karolanden, Lao Pengulu, *bb* 12503 (BO); Langkat, Sungei Sedapan, *bb* 9132 (BO); Tasik, *Koorders* 10456 (BO). INDRAGIRI: Keritang, *bb* 28660 (BO, L, SING); Kuantan, Djake, *bb* 26487, 26491 (BO, L); Kuantan, Sungei Besar, *bb* 24028 (BO, L); Peranap, *bb* 30102, 30120 (A, BO, L). DJAMBI: Muara Pidjuan, *bb* 12273 (BO, L, ♂). BENKULEN: Redjang, Penandjung pandang, *bb* 2735 (BO, L). PALEMBANG: *Praetorius s.n.* (L); Banjuasin and Kubustreken, *Grashoff* 809 (BO, L); Banjuasin and Kubustreken, Bajunglintjir, *NIFS T* 27 (BO, L, ♂, ♀), 195 (BO, K, L, SING, ♂, ♀); Komering Ulu, *Grashoff* 575 (BO); Lematang Ilir, Gunong Magang, *NIFS T* 284 (BO, L, P, SING, U, ♂, ♀), 300 (BO, L, ♂), 522 (BO, ♂); Lematang Ilir, Semangus, *bb* 32245 (BO, L); Muara Dua, *Grashoff* 461 (BO, L); Muara Dua, Kisau, *bb* 9630 (BO); Muara Mengkulem, *Forbes* 3041 (A, BM, CAL, L, P, SING, ♂, ♀); Musi Ilir, Ipil, *NIFS T* 1071 (BO, L); Rawas, *Grashoff* 1032 (BO, L); Pasemahlanden, Djangkar, *bb* 8106 (BO). LAMPONGS: Mangala, *Gusdorf* 47 (BO, ♂, ♀), *Teysmann HB* 4358 (BO, L, U), 4369 (P), 4393 (BO, L, U), 4419 (BO, U); Seputik, Suwikis, *bb* 2844 (BO, L); Seputik, Tulangbawang, Gunong Sugit, *Gusdorf* 140 (BO, ♀). SIMALUR: *Achmad* 814 (BO); Landschap

Tapah, Defajan, *Achmad* 1429 (BO, K, L, U). BANKA: *Teysmann HB* 3296 (BO), 6844 (BO, K, L, P); Blinju, *Grashoff* 14 (BO, L, ♂, ♀); Blinju, foot of Gunong Rengkuk, *Berkhout* 149a (BO); Djebus, *Teysmann HB* 3369 (BO, U), 7243 (L), 7252 (C, L, P); Lobok-besar, *Kostermans & Anta* 824 (A, K, ♂); Muntok, Majang, *bb* 7596 (BO); Toboali, *Teysmann HB* 7265 (BO, P); Tohrin, *sine nom. HB* 296 (U). BILLITON: *Rossum* 20 (BO, K, L, ♂), 76 (BO), *Teysmann HB* 17580, 17583 (BO); Tandjong Pandjang, *bb* 6778 (BO). RIOUW ARCHIP.: Tandjong Pinang, Bintan, *Teysmann HB* 7284 (BO, C, L, P). LINGGA ARCHIP. NIFS Ri./I-128 (BO). P. Singkep: Marok Tuwa, near Sungei Lorong, *Amat* 12 (L); Ulu Sungei Marok Tuwa, *Amat* 34 (BO, L).

Borneo. SARAWAK. *Beccari PB* 2478 (K, P, ♂), 2998 (K, P, ♀); near Kuching, *Haviland* 1888 (CAL, K, ♀); Mt. Poi, *Clemens* 20305 (K, NY); Sibuan Sungei Assan, *For. Dept. Sarawak S* 0502 (SAR). WEST BORNEO. Melawie, Tjatit B. Tangkujung, *bb* 26439 (BO, L); Sadakan, Pait, *bb* 8048 (BO, L). SOUTH AND SOUTHEAST BORNEO. Martapura, Djungur, *bb* 10384 (BO); Pleihari, Sungei Sangga, *bb* 9950 (BO); Tanah Bumbu, Kampong Baru, *bb* 13356 (BO, L, ♂, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Sangkulirang, Ranggung, *bb* 7968 (BO); Tandjong Bangko region, mouth of Mahakam River, *Kostermans* 7186 (K, L, ♀). W. Kutei: Djembajan, Sungei Kelasan, *bb* 25122 (BO, L); Djembajan, Sungei Gitan, *bb* 12766 (BO); Tandjong Tsue, *Endert* 1953 (A, K, L). BRITISH NORTH BORNEO. Elphinstone prov., Tawao, *Elmer* 21514 (A, BM, BO, C, GH, K, L, P, SING, U, ♀). P. LAUT. Sungei Paring, *bb* 12897 (BO, U, ♂, ♀), 13258 (BO).

Java. *Blume* 1364 (CAL, L, ♀), *Reinwardt s.n.* (L), *De Vriese* 1655 (L). WEST JAVA. Batavia: Depok, *Beumée* 6021, *Hallier s.n.*, Aug. 1896 (BO), *Koorders* 31077 (BO, L), 41048 (BO, ♀), 42776 (BO), 42792 (BO, ♂), 44119 (BO), *Van Steenis* 12750 (L); between Kota Bambu and Djembatan duren, *Backer s.n.*, 1902 (BO, ♂); Leeuwiliang, Pasir Angsana, *Bakh. van den Brink* 6974 (BO, K, L, ♂, ♀); Leeuwiliang, Pasir Tjihideung, *Bakh. van den Brink* 6386 (BO, L); Leeuwiliang, Tjibata, *Bakh. van den Brink* 6796 (BO, L, ♀); Tjiampea, *Koorders* 30364, 30365 (BO), 30366 (A, BO, L, ♂). Buitenzorg: Handjere, Janglappa, *NIFS Ja* 6206 (L). Cheribon: Kuningan, *Houter* 67, 138 (BO). Preanger: Palabuanratu, *Koorders* 8738 (BO, L), 12561, 12562 (BO, L, ♂), 12570 (A, BO, L, P, ♂, ♀), 15677 (BO, L, ♂), 33049 (BO); Palabuanratu, Buniwangi, *sine nom. et num.*, Mar. 1873 (BO); Palabuanratu, Tjibareno, *Winckel* 1858 (BO, L, U, ♀); Sanggrawa, *Koorders* 8739 (BO). CENTRAL JAVA. Pekalongan: Loutresten, E. Tegal, *Beumée* 1889 (BO); Pemalong, *Bruscomps* 8 (BO). NUSA KAMBANGAN: Tjilatjap. *Koorders* 27032 (BO, ♀). Lesser Sunda Islands. Bali: [? cult.] *sine nom. et num.* (L).

Cultivated. INDIA: Calcutta, Hort. Bot., *Wallich* 2142 (P), 4658D (BM, CGE, K), *s.n.*, 1819 (BM, ♂, ♀). JAVA: Bantam, *Zollinger* 1009 (A, L, P, U); Bogor, Hort. Bot., *Zollinger* 2982 (BM, P, U, ♀). Unlocalized collections: *Abel s.n.* (East Indies) (K, ♀); *Kurz* 2084 (CAL); *Roxburgh s.n.* (BM).

The synonyms given above all refer exclusively to *Artocarpus rigidus* ssp. *rigidus*, as do the references, except for King's descriptions (1888, 1889) which include *A. hispidus*. Merrill (*Jour. Arnold Arb.* 19: 331. 1938) reduced *A. rigidus* to *A. rotunda* (Houtt.) Panzer, *Pflanzensyst.* 10: 380. 1783, based on *Rademachia rotunda* Houtt. *Nat. Hist.* II. Pl. 11: 455. 1779, which was very briefly described from Javan material as having leaves of the same shape as *Artocarpus integer* but without "roughness"

except on the fruit, which was round and grew, so Houttuyn was told, to the size of a child's head. This could be a crude description of *A. rigidus* but, in fact the leaves in this species are more or less scabrid beneath, the twigs and peduncles are appressed-hispid and the syncarp is smaller. Since no type has been found at Leiden, the identification would have to be based primarily on the vernacular name *Mandelique* given by Houttuyn, which is cited by Teysmann and Binnendijk (Cat. Bog. 85. 1866) and by Koorders and Valetton (1906) as a Javan name for *A. rigidus*. The description does not fit any other species occurring in Java and it seems preferable to treat *A. rotunda* as a *nomen dubium*.

The specimen listed above from Bali is probably from a cultivated tree, since there are no other records of *A. rigidus* from eastern Java or the Lesser Sunda Islands as an indigenous plant. One of the collections from Penang, *Curtis s.n.*, May 1894, has the syncarp processes softly pubescent, but otherwise agrees with *A. rigidus* ssp. *rigidus*.

ssp. *asperulus* (Gagnep.) Jarrett, stat. nov.

Artocarpus calophylla Kurz, Prelim. Rep. For. Pegu App. A, 124, App. B, 82. 1876. in clavis, For. Fl. Burma 2: 431. 1877, non Teysm. & Binnend., 1866, quae est nomen nudum; King in Hook. f. Fl. Brit. Ind. 5: 540. 1888; King, Ann. Bot. Gard. Calcutta 2: 8. t. 2. 1889. Holotype, Burma, *Kurz s.n.* (CAL).

Artocarpus asperula Gagnep. Bull. Bot. Soc. Fr. 73: 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 734. fig. 90. 1928. Syntypes, Indochina, *Chevalier 30083*, *Herb. For. Cambodge 36930*, *Pierre 15*, 1851, *Poilane 6644*, *Thorel 1067* (P); lectotype, *Poilane 6644* (P).

Artocarpus asperula var. *hirta* Gagnep. Bull. Soc. Bot. Fr. 73: 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 735. 1928. Syntypes, Indochina, *Pierre 3377*, *3777*, *Thorel s.n.*, 1862-66 (P); lectotype, *Pierre 3777* (P).

Artocarpus chaplasha auct. non Roxb., Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 735. 1928.

Differs from ssp. *rigidus* as follows: *twigs* rather softly and densely sub-appressed hispid-pubescent, juvenile shoots with long patent hairs; *leaves* obovate-oblong to ovate, base rounded or shallowly cordate, rarely cuneate; very shortly appressed-hispid above, rarely nearly smooth, indumentum beneath as on shoot; lateral veins 9-12 pairs; *syncarp* with processes hispid from spreading hairs c. 0.5 mm. long.

VERNACULAR NAMES: *Taung peing*, Burma; *Kanun pan*, Siam; *Knol prey* or *Knor prey*, Cambodia; *Cay mit nai* or *Mit nai*, Annam. USES: as in ssp. *rigidus*.

DISTRIBUTION: in evergreen forest to 3000 ft., Burma, Siam, Indochina.

Burma. Kyauktwin [not located], *Meebold 15599* (CAL). TENASSERIM. Amherst: *Falconer 1015* (CAL, ♀); Mekhrein chaung, *Parkinson 5205* (DD, ♀); Moulmein, *Kurz s.n.* (CAL). Tavoy: Kalemaung Res., *Ba-Pe 864* (CAL, DD, ♀); Kadwe For. Circle, *Manson 762* (CAL, ♀). **Siam.** Chantaburi [Chantaburi?], Makham, Khao sabap, *Put 2368* (CGE); Rayawng, Ban Pe, *Kerr 2734* (BM, ♀); Kaw Chang (island off se. coast), Klawng Mayom, *Kerr 6923* (BM, P, ♀), *Marcant 1329* (BM, ♀). PENINSULAR SIAM. Surat, *Sman 2365* (CGE, ♂, ♀); Surat,

Panom, *Kerr* 12375 (BM, ♀). Island off w. coast: P. Terutao, *Kerr* 14198 (BM, ♀). Islands off e. coast: Kaw Pa-ngan, *Kerr* 1235 (BM, ♀); Kaw Tao, *Kerr* 12799 (BM, ♂).

Indochina. CAMBODIA: *Hahn* 61 (P); Kamput, *Pierre* 15 (P); Phom-ba, Nem-Tram-Kok, *Müller* 350 (P); Pursat Prov., Pnom Barong, Roleap, *Herb. For. Cambodge* 36930 (P). COCHINCHINA. *Thorel* 1067 (A, BM, K, P, ♂, ♀), *Thorel s.n.*, 1862-6 (P). Baria prov.: *Chevalier* 36637 (P), *Commission de la Gutta* 4 (P); Xuon moc, *Chevalier* 36606 (P, ♀). Bien Hoa prov.: *Commission de la Gutta s.n.*, 1866 (P); Bao Chiang, *Pierre* 1851, p.p. (A, BM, K, P, ♀); Song lu, *Pierre* 3777 (A, P); Trang-bom, *Chevalier* 30083 (P, ♀), *Chevalier* 36761 (P), *Fleury* 39323 (P, ♀). Budot, *Müller* 1728 (P). Saigon [? cult.], *Pierre* 3377 (P, ♀). Tay ninh prov., Cay Cing, *Pierre* 1851, p.p. (L). ANNAM: Massif de la Mère et l'Enfant, *Poilane* 6644 (K, P, ♀). P. CONDORE: *Perry* 4699 (P).

This subspecies is consistently distinguished from the type by the hispid and not hispidulous syncarp processes, and usually also by the rounded or shallowly cordate base and rough upper surface of the leaves. In indumentum and leaf shape it is rather variable, though the hairs are usually denser and softer on both shoot and leaf than in *ssp. rigidus*. The latter feature is most marked in Burma, where, in addition, the leaves are frequently ovate. This form was described by Kurz as *A. calophylla* and is shown in King's plate (1889), drawn from *Falconer* 1015 and not Kurz's own collection, as stated by King, who reversed these two collections in his discussion of the species. In Siam and Indochina the leaf shape is usually obovate-oblong and the form was described by Gagnepain as *A. asperula*. However, since the variation between the two forms is continuous, they are here united. Both species were distinguished by their authors from *A. rigidus* by the indumentum of the leaf, but, since the differences in this and in the leaf shape are not constant and those in the syncarp are so slight, it is preferable to treat the continental entity as a geographical subspecies of *A. rigidus*. The northern boundary of Malaya appears to separate the two subspecies, with the exception of Helfer's collection of *ssp. rigidus* from Tenasserim, but more material from this area is desirable to show whether there is any intergrading of characters.

Gagnepain's *A. asperula* var. *hirta* was described from sapling collections with long patent hairs on the shoot. Two Indochinese collections of *A. rigidus* *ssp. asperulus* at Paris, *Comm. de la Gutta s.n.*, 1866, and *Pierre* 15, were labelled *A. polyphema* Pers., but the native species which may have been included by Loureiro in his confused description of *Polyphema champeden*, on which this name is based, is not identifiable, although it will be further discussed under *Artocarpus integer*. The identification was not mentioned by Gagnepain in 1928.

(To be continued)